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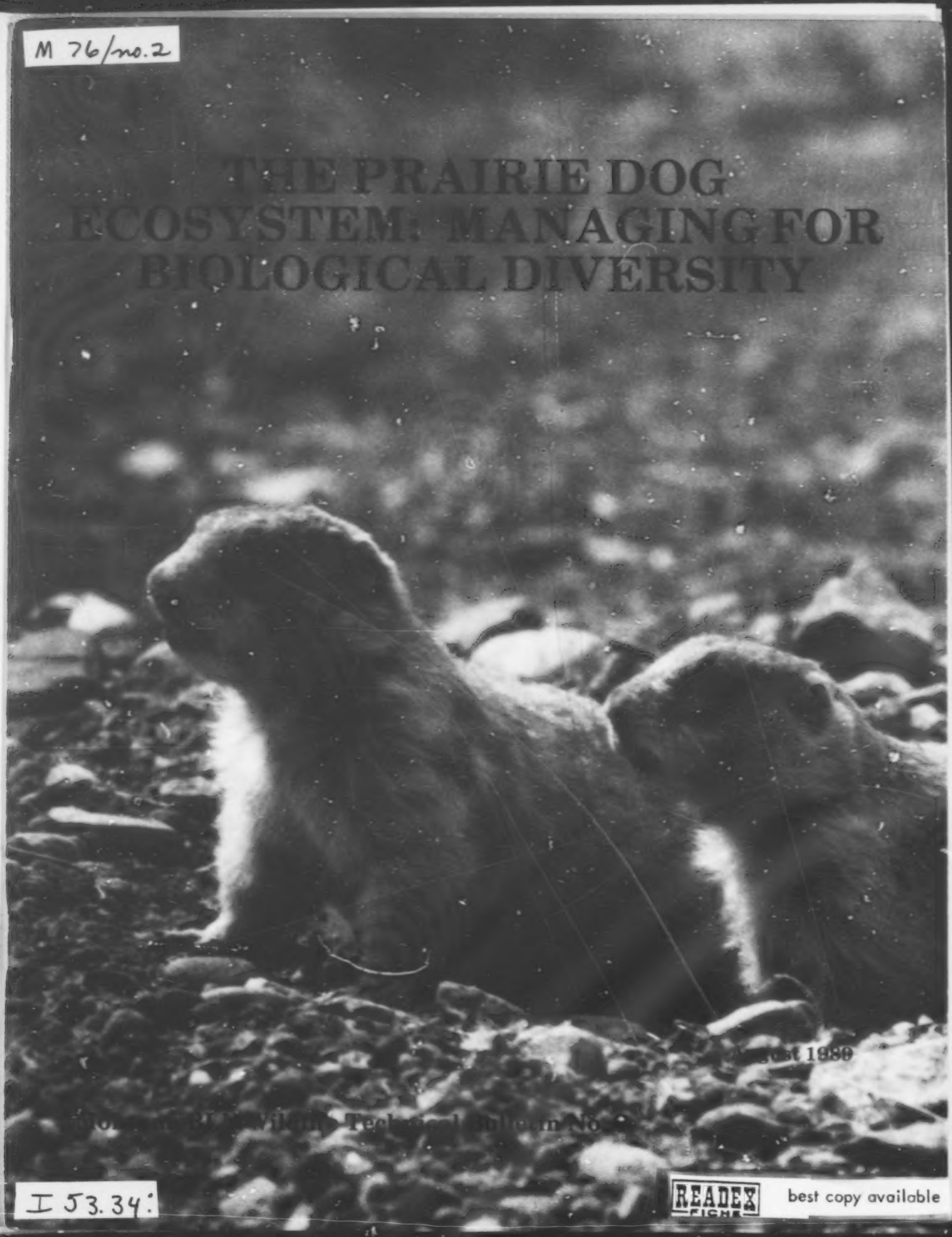
THE PRAIRIE DOG ECOSYSTEM: MANAGING FOR BIOLOGICAL DIVERSITY



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THE PRAIRIE DOG ECOSYSTEM: MANAGING FOR BIOLOGICAL DIVERSITY

Montana BLM Wildlife Technical Bulletin No. 2

August 1989

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EDITORS' INTRODUCTION

Tim W. Clark, Dan K. Hinckley, and Terrel Rich

The prairie dog ecosystem is that assemblage of species and ecological processes associated with prairie dog colonies. Over 100 vertebrate species are known to use prairie dog colonies as habitat. Some of these species are nearly totally dependent on prairie dogs, such as the black-footed ferret (*Mustela nigripes*); others clearly benefit from their relationship, such as ferruginous hawks (*Buteo regalis*); and still others are minimally associated, such as the horned lark (*Eremophila alpestris*). This biological diversity includes a variety of predator-prey relationships and competitive interactions.

The conservation of biological diversity (or biodiversity) is a growing national priority. There are already 29 Congressional Acts that call for or support the maintenance of biodiversity. Biodiversity, according to the Office of Technology Assessment (1986:1) ". . . refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequencies. For biological diversity, these items are organized at many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis for heredity. Thus, the term encompasses different ecosystems, species, genes, and their relative abundance."

This living diversity is the source of evolutionary adaptation and is fundamental to all ecological processes. It has many utilitarian as well as aesthetic, educational, research, recreational, cultural heritage, and economic benefits. Conservation of biodiversity is receiving increasing scientific and management attention (e.g., Soule 1986; Simberloff 1988). Management to perpetuate biodiversity is the only way to ensure conservation of our living natural heritage.

Historically, the five species of prairie dogs occupied millions of acres of grasslands and intermountain basins of western North America from Mexico to Canada. Today, their numbers and range have been drastically reduced. Future management for the maintenance of biological diversity in the prairie dog ecosystem will depend on adequate research about this complex of species and their environmental relationships. This volume was prepared to support this goal — management for the conservation of biological diversity of the prairie dog ecosystem.

This volume is just one step toward this goal. Besides encouraging appropriate management, this Technical Bulletin is a partial progress report on work carried out in Montana between mid 1983 and early 1989 towards those research ends, with special reference to restoration of the endangered black-footed ferret (see Clark 1986; Flath and Clark 1989).

The Montana program focused on black-footed ferret recovery and overall management of the prairie dog ecosystem. It is a product of the close working relationship developed over the last 5 years among Montana Department of Fish, Wildlife and Parks, Bureau of Land Management, U.S. Fish and Wildlife Service, U.S. Forest Service, Montana Department of Agriculture, Animal and Plant Health Inspection Service, Bureau of Indian Affairs, Indian Reservations, Biota Research and Consulting, and Northern Rockies Conservation Cooperative (see Clark et al., in press). Additionally, it has involved volunteers from Yale University, Montana State University, and University of Montana. The program is funded via Endangered Species Act Section 6, standard agency budgets, and grants from World Wildlife Fund—US, Wildlife Preservation Trust International, Chicago Zoological Society, New York Zoological Society, Fanwood Foundation, Merril G. and Emita E. Hastings Foundation, Nu Lambda Trust, Tom and Sybil Wiancko, Lost Arrow Foundation, Cathy Patrick Foundation, and other private sources to the Northern Rockies Conservation Cooperative. The cooperation and support of all these organizations and individuals was essential.

This bulletin has two companion volumes: (1) Annotated prairie dog bibliography 1973 to 1985. Montana BLM Wildlife Technical Bulletin No. 1. Tim W. Clark, 32 pp., and (2) Montana prairie dog management guidelines. Montana BLM. Montana Black-Footed Ferret Working Group. 14 pp. Additionally, several technical publications support this Technical Bulletin (e.g., Flath and Clark 1986, Clark, In Press) by providing background or supporting information.

We would like to thank the 9 authors and the 18 plus reviewers who contributed to this publication. Besides the individual contributors and the organizations and agencies that supported this work, several other individuals have played important roles: Ron Crete and Bill Haglan of the US Fish and Wildlife Service, and Dan Bricco and Chris Erb of the Bureau of Land Management. We thank you all.

Tim W. Clark, Dan K. Hinckley and Terrel Rich, Editors
August, 1989

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INTRODUCTION

Dennis L. Flath, John D. Cada and Arnold R. Dood

Prairie dog management is a controversial topic due to the complexity and misunderstanding of ecological relationships involved in the "prairie dog ecosystem." Responsible management, addressing both biological needs and socio-political demands, will require cooperation, hard work, and creativity in the long term. This bulletin addresses unique responsibilities and new opportunities in wildlife management that have not yet been confronted.

In Montana, comprehensive statewide inventories of the prairie dog resource began in earnest in 1983, although John Grensten (BLM) began systematic surveys prior to this in Phillips County. Black-footed ferret searches served as a driving force in these efforts, but other ecological values were also documented. Despite the obvious importance of ferrets, they are treated as a component of the prairie dog ecosystem in our *Montana Prairie Dog Management Guidelines* (Montana Black-footed Ferret Working Group, 1988), and involved persons have never lost sight of other values. Similarly, social, political, and economic concerns have been and will continue to be a major influence on management direction.

The efforts in Montana from the very beginning have been carried out within the context of a national priority. Desire to stimulate similar progress in other states provided the impetus to form the Interstate Coordinating Committee in 1987 dealing with the mechanics of ferret recovery and associated prairie dog management. Data generated thus far in Montana has helped open new opportunities nationwide.

Much of the success to date stems from use of the Working Group approach where a variety of agencies and people are involved (Clark, et al., 1989; and Clark and Cragun, in press). This joint effort has resulted in close coordination and efficient use of resources. Success of the Montana Black-footed Ferret Working Group is a credit to all those agencies and participants who have contributed their time. The ultimate reward, however, will certainly be establishment and recovery of a viable (i.e., functional) ferret population within the context of a viable and dynamic prairie dog ecosystem. For wildlife and resource managers who have the vision to recognize and capitalize on opportunities, these are exciting times indeed.

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Prairie Dog Colony Location Surveys and Black-footed Ferret Searches In Montana

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Abstract.—Searches to locate black-footed ferret (*Mustela nigripes*) populations and their potential habitat represented by prairie dog (*Cynomys* spp.) colonies were conducted in Montana between 1984 and 1989. The locations of 700+ prairie dog colonies totalling more than 100,000 ac (~40,500 ha) were discovered with about 77 percent comprising 8 general concentration areas. Sightings of black-footed ferrets were solicited from the public by appealing to their interests (Pre-Reward Program) and by monetary incentives (Reward Program). Pre-reward efforts (August 1986 and later) generated 69 reports of which only 21 were considered possible black-footed ferrets. The Reward Program (August 1986 and later) generated an additional 66 reports, of which 10 were possible black-footed ferret sightings. All possible ferret sightings were followed up with field searches. Only one report was confirmed to have involved a live black-footed ferret (1977 in Carter County). The finding of one ferret cranium from Fort Belknap Indian Reservation was documented. Five specific areas were identified as having relatively high potential of supporting black-footed ferret populations. These areas, which represented about 34,500 ac (~14,000 ha), were searched employing nocturnal summer and/or diurnal winter surveys for a total of 170 person days. Additionally, numerous short-term ferret searches totalling 50 person days were conducted statewide on about 7,000 ac (2,832 ha) of colonies. Searches produced no evidence of current ferret presence but yielded skeletal material from 2 individual ferrets in Carter County on the same 2,500 ac (1,011 ha) colony which produced the confirmed ferret sighting.

Prairie dog colonies represent habitat for a diverse complement of vertebrate, invertebrate, and plant species (Koford 1958; Tyler 1968; Campbell and Clark 1981; Clark et al. 1982; Agnew 1983; Reading et al. 1989), and the biodiversity associated with these colonies is characteristically greater than the surrounding environs (Hansen and Gold 1977). Some species, such as the endangered black-footed ferret (BFF), are nearly totally dependent upon the habitat provided by these colonies (Forrest et al., 1985; Minta and Clark 1989). BFFs rely on prairie dogs as their major prey source (Sheets et al. 1972; Campbell et al. 1987) and as creators of the cover (burrow systems) necessary for survival (Hillman 1968; Henderson et al., 1969; Linder et al., 1972). Therefore, all active prairie dog colonies serve as potential BFF habitat. In order to preserve any existing populations of BFFs, or assist in recovery efforts of the species, it is critical first to identify and then to manage prairie dog ecosystems effectively.

This paper describes efforts and results of extensive prairie dog colony surveys and intensive BFF searches throughout Montana between 1984 and 1989. These surveys and searches were conducted primarily to discover one or more populations of BFFs. An important offshoot, however, was to document the extent of the prairie dog ecosystem which so many other species of wildlife rely upon. This information will assist land managers in developing long-range management plans for prairie dog ecosystems and specifically for those associated species whose existence may be threatened, endangered, or of special concern.

LOCATION OF PRAIRIE DOG COLONIES

Initial efforts to identify potential BFF habitat in Montana began in 1984 by compiling all known locations of white-tailed (*C. leucurus*) and black-tailed (*C. ludovicianus*) prairie dog colonies in the state. A variety of federal and state agencies involved with land and/or wildlife management were contacted and this effort continued throughout the period of study. These agencies included:

Montana Department of Fish, Wildlife, and Parks (MFWP);
Bureau of Land Management (BLM);
U.S. Forest Service (USFS);
U.S. Fish and Wildlife Service (USFWS);
USFWS-Refuge System (USFWS-RS).
Bureau of Indian Affairs-Indian Reservations (BIA);
Montana Department of Agriculture (MDA).

Private landowners and individuals who lived in areas of known prairie dog distribution or who were believed to know about prairie dog colony locations (e.g., trappers, hunters) were also contacted. Several private businesses (e.g., environmental consulting companies) were solicited as well. These initial contacts led to the formation of the Montana Black-footed Ferret Working Group in 1984 consisting of one or more representatives of all these agencies, as well as Biota Research and Consulting (Montana Black-footed Ferret Working Group 1988).

The locations of previously undiscovered prairie dog colonies were also sought. After plotting known colonies on a base map, we surveyed areas where apparent data gaps existed. Colony searches were conducted by Biota, MFWP, BLM, BIA, USFS, and USFWS via aerial and ground surveys with varying degrees of intensity and success.

Colony locations were plotted on maps of three different scales. A base map of 1/8 inch to the mile was used to plot the general locations of all colonies and allowed the identification of complexes and data gaps. Clark et al. (1987) defined a prairie dog colony complex as two or more colonies totalling at least 1,360 ac (550 ha) within 1.9 mi (3 km). In addition, colonies were precisely mapped on BLM 1/2 inch to the mile and USGS 7.5 or 15 min topographic maps for field and office use.

Historical information about age of colonies and complexes, degree to which colonies were subjected to control efforts, and the presence of disease was collected whenever possible. This information was believed important in determining the potential for BFF presence. Regardless of their present size and degree of activity, complexes which had historically been reduced to very low population levels

by control efforts, disease, or other factors, would likely have resulted in BFF extirpation from those areas.

Results — Over 700 active prairie dog colonies totalling over 100,000 ac (40,470 ha) were located. About 500 colonies had been previously identified by land and wildlife managers, private groups, and individuals, and about 200 colonies were located during the searches for additional colonies. The BLM, Biota, and USFWS surveys were especially productive in locating new colonies.

Eight general areas with large concentrations of active prairie dog colonies were identified, comprising about 77 percent of the prairie dog colonies in Montana:

(1) southern Phillips County, ~24,000 ac (~9,700 ha) of prairie dogs;
(2) Fort Belknap Indian Reservation, ~12,000 ac (~4,850 ha);
(3) northeast Garfield County, ~4,500 ac (~1,820 ha);
(4) southern Custer County, ~16,500 ac (~6,677 ha);
(5) southern Prairie/extreme northern Custer County, ~6,000 ac (~2,428 ha);
(6) northern Carter County, ~5,000 ac (~2,023 ha);
(7) southwestern Valley County, ~3,000 ac (~1,214 ha); and
(8) Tongue River area, ~6,000 ac (~2,428 ha).

These concentrations served as initial areas where BFF search efforts were expended.

BLACK-FOOTED FERRET SIGHTINGS

Background

Determined efforts to gather information on BFF distribution and to solicit BFF sightings began in 1974 by Tim W. Clark under a grant from the National Geographic Society. Although centered in Wyoming, reports were collected from throughout historic BFF range. He solicited reports in various rural settings, contacting appropriate agency personnel, publicized efforts in newspapers, regional, and national magazines, television and radio public service announcements, and offered a $50 reward for information leading to the discovery of BFFs in the wild (T.W. Clark, personal communication). Wanted posters describing this program were widely distributed and, in 1980, the reward was increased to $250. The reward was paid out only once—to the finders of BFFs in Meeteetse, Wyoming, although this program was not directly responsible for that discovery.

Following completion of the original BFF Recovery Plan in 1978, it became apparent to Recovery Team members that the present distribution of BFFs was unknown. Jobman and Anderson (1981) attempted to fill this void by soliciting BFF sightings from 62 state, federal, provincial, and private sources for the period 1970-1981. Their effort is ongoing and updates are distributed annually.

Montana Pre-Reward Program

The 1981 discovery of BFFs in Meeteetse, Wyoming, and the press coverage associated with this event revived interest in BFFs in states throughout their historic range. State fish and game departments immediately began receiving increased numbers of BFF sighting reports. In 1983, in response to a commitment by MFWP to search for BFFs in Montana and a dramatic increase in the number of BFF sightings being reported, the MFWP and Biota developed a reporting system designed to standardize and assess BFF sightings. This system included a standardized reporting form (Appendix 1), criteria to evaluate each BFF sighting (Appendix 2), and a protocol to follow if BFFs were subsequently discovered. Similar efforts were initiated in other states.

All persons reporting BFF sightings were interviewed. Initial interviews were conducted via phone by one of several cooperators. BFF sighting forms were completed during this initial interview. If the sighting warranted it, the individual was then interviewed in person as soon as possible to confirm earlier statements and gather more detailed information using field guides, pictures, and maps. This interview was typically conducted by a Biota or MFWP representative. If the sighting continued to show high potential, a site visit was made to assess the BFF habitat in the sighting area. Intensive BFF searches were conducted if suitable habitat existed. In the case of sightings which were not field searched by trained personnel, the individuals were strongly encouraged to make follow-up efforts themselves.

Results — In the period preceding August 1986, 69 BFF sightings were reported to the MFWP. Twenty-nine (42 percent) sightings were determined to involve an animal other than a BFF based on interviews and nothing more was done with them. These sightings involved an unknown, non-BFF species (N=24, 83 percent), long-tailed weasels (*Mustela frenata*, N=3, 10 percent), a mink (*M. vison*, N=1), and 1 set of misidentified badger (*Taxidea taxus*) or prairie dog diggings. Forty (58 percent) sightings warranted additional interviews and/or field searches. Thirteen (33 percent) of these were an unknown species, 3 (7 percent) were long-tailed weasels, 1 (3 percent) involved tracks of an unknown animal, 21 (53 percent) were possible BFFs, and 2 (5 percent) involved confirmed BFF skeletal material. All 21 possible BFF sightings and the two skull finds (Figure 1) were field checked and three of them confirmed recent BFF presence. One sighting, involving a live BFF, was made near Ekalaka in 1977, and confirming evidence in the form of 1 cranium with mandible and a second mandible from a different BFF was found by Biota personnel in 1984. The only other confirmed evidence of past BFF presence was a skull found on Fort Belknap Indian Reservation by Craig Knowles in 1983 (Clark et al. 1987).

Montana Reward Program

In late 1985, it became apparent to participants in the Montana BFF studies that the number of BFF reports had decreased dramatically from past levels. It was unclear whether solicitation efforts had: (1) worked so well that all or most sightings had been obtained, (2) that more publicity was necessary to reached untapped sources of sightings, (3) that more incentive was necessary to get more people to report BFF sightings, or (4) some combination of the above or other reasons.

BFF study cooperators determined that a combination of increased publicity and monetary incentives would likely result in more BFF reports. To accomplish this, a reward program to be administered by the MFWP was initiated in August 1986. A $5,000 reward for information leading to the discovery of a wild population of BFFs in Montana was generously offered by the New York Zoological Society/Wildlife Conservation International (NYZS/WCI). Another expected benefit of this program was to

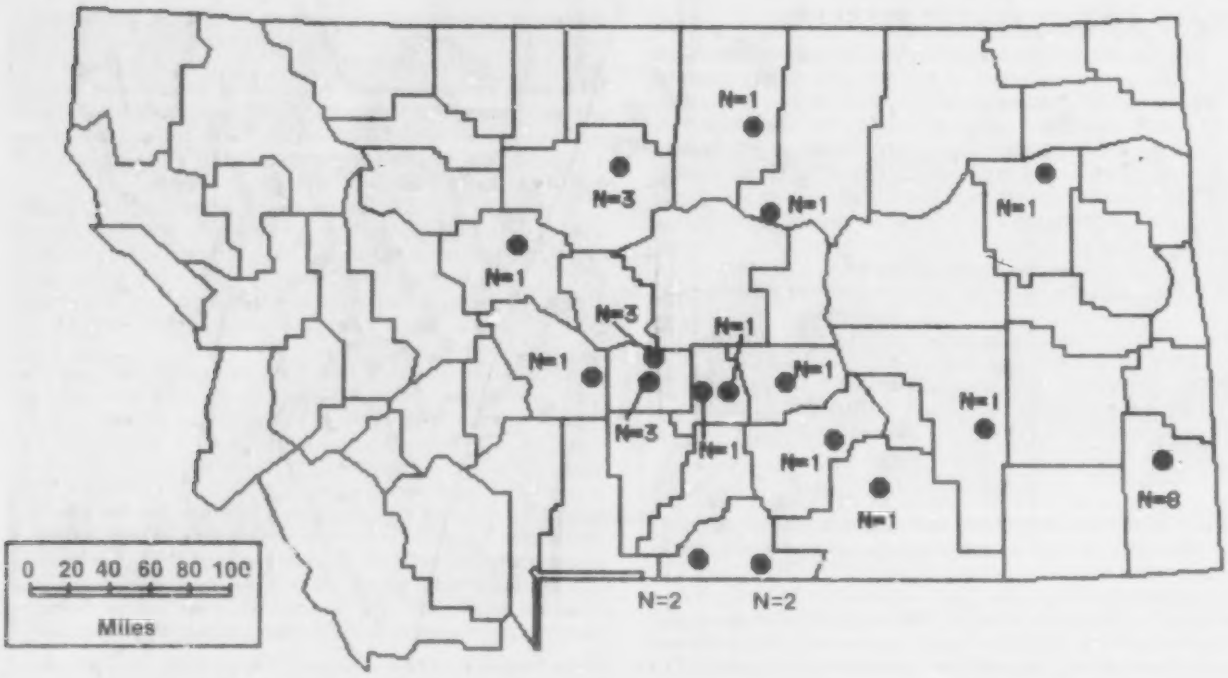


Figure 1.—Locations of 32 possible black-footed ferret sightings generated by the Pre-Reward and Reward Program in Montana.

place more responsibility on the person making the report and thereby reserving limited funds for follow-up of reports with high potential.

An identical offer of reward funds was offered to Wyoming by NYZS/WCI in early April 1986 (Captive Breeding Specialist Group 1986a). However, the Wyoming Game and Fish Department (WGFD) initially opposed the Reward Program for reasons listed in Belitsky (1986). Concerns primarily centered around not being able to adequately respond to large numbers of sightings, negative public opinion when sightings failed to produce BFFs, and that Meeteetse BFFs might be illegally removed (Belitsky 1986). The decision of WGFD was not to participate in a reward program at that time (Captive Breeding Specialist Group 1986b), but instead to use the Montana program as a test case and to follow their efforts closely (B. Oakleaf 1989, WGFD, personal communication). In January 1987, WGFD decided to participate in the reward program when the feared problems never developed (B. Oakleaf 1989, WGFD, personal communication).

Exhaustive efforts were made by members of the BFF Study Group to publicize the Montana reward program. This included local and regional newspaper releases and articles, television and radio public service announcements, articles in popular regional and national magazines, and the distribution of "wanted posters" describing BFFs and the program in rural and urban post offices, cafes, bars, grocery stores, sporting good stores, etc.

Results — To date, the Reward Program, which is still in effect, has generated 66 BFF sightings. Thirty-nine (59 percent) sightings were determined to have very low potential of involving a BFF based on interviews and were not followed up. Of these, 17 (43 percent) involved suspected long-tailed weasels, 15 (38 percent) involved an unknown, non BFF species, 4 (10 percent) involved domestic ferrets (*Putorius* spp.), 1 (3 percent) was a badger, 1 (3 percent) was a pine marten (*Martes americana*), and 1 (3 percent) involved misidentified badger or prairie dog diggings. Twenty-seven sightings (41 percent) warranted subsequent follow-up. Of these, 11 (41 percent) involved suspected long-tailed weasels, 3 (11 percent) involved domestic ferrets, 3 (11 percent) involved an unknown species, and 10 (37 percent) were possible BFFs. Field searches conducted in areas where these 10 possible BFFs were sighted (Figure 1) failed to produce any evidence of current presence.

National Reward Program

Following the success of the Montana Reward Program in generating BFF sightings, the Black-footed Ferret Interstate Coordinating Committee (BFFICC) (1987) identified the need for a national reward program and recommended the USFWS establish a program following that used by Montana. Presently, a $5,000 National Reward Program is in effect and participants include Montana, Wyoming, Utah, Colorado, Nebraska, South Dakota, Texas, Oklahoma, Kansas, and the Navajo Nation (in Arizona and New Mexico). Those states not participating include New Mexico, Arizona, and North Dakota, although the latter two actively participate in BFFICC. Efforts to increase the award to $10,000 using NYZS/WCI funds are presently underway (L. Hanebury, USFWS, personal communication).

BLACK-FOOTED FERRET SEARCHES

Prairie dog colonies were ranked for subsequent intensive BFF searches based on colony and colony complex characteristics, documented BFF observations in the area, and recent confirmed or unconfirmed BFF sightings.

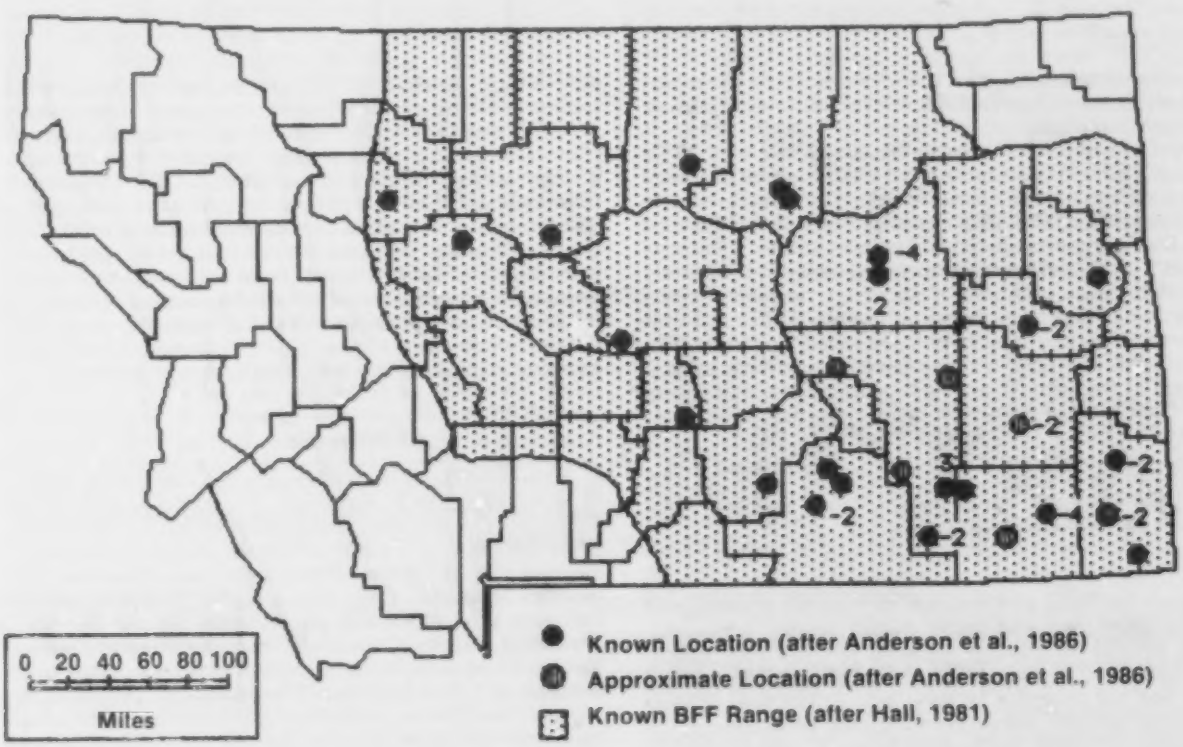
Colony attributes were assessed during and following location efforts using methods described by Houston et al. (1986). These included size of the complex, number of colonies, size of individual colonies, intercolony distances, degree of activity, poisoning and disease history. Although the Habitat Suitability Model (HSI) detailed by Houston et al. (1986) was in its developmental phase during early search efforts (i.e., 1984-1985), researchers realized the influence these attributes would have on determining BFF presence from their experience studying BFFs in Meeteetse. Therefore, data were collected on these attributes and used them either intuitively during initial efforts, or subjected them to analysis via the HSI model during later phases in ranking BFF search areas.

Information on documented BFF observations, primarily museum and private collection specimens, was collected. Anderson et al. (1986) summarized these specimens for Montana as well as for other states and provinces in former BFF range and Figure 2 shows the distribution of their results in Montana. They reported 44 BFF specimens collected in Montana between 1877 and 1984. Interestingly, fully 64 percent (N=28) of these specimens were collected during a 10-year period between 1915-1924, while only 7 percent (N=3) were collected pre-1915 and 29 percent (N=13) post-1924 (Anderson et al. 1986). The period between 1915 and 1924 coincides with exhaustive prairie dog control efforts throughout Montana (Flath and Clark 1986). Three specimens, all skeletal material, were collected between 1983 and 1984 and this recent proof of BFF presence significantly influenced subsequent search efforts.

Recent BFF sightings, as described earlier, were important in determining high priority areas to search. If reports rated high after being subjected to the evaluation process, efforts were immediately made to verify the presence of BFFs. When localized areas showed a history of repeated BFF sightings, these areas also received a high priority for subsequent search efforts.

Once an area was selected for intensive BFF surveys, certain colonies within this area or complex were selected (based on size and activity) to serve as samples of the complex. The rationale was that if a BFF population was present within this complex, BFFs should be present on the largest and most active colonies within that complex. This sampling scheme was developed because limited funding prohibited exhaustively searching every colony within a given complex for BFF. It was realized that if extremely low population numbers existed on these complexes and animals were confined to smaller, less active colonies within a given complex, BFF presence might go undetected

Figure 2.—Known and approximate locations of black-footed ferret specimens collected in Montana between 1877 and 1984.


0 20 40 60 80 100
Miles
Known Location (after Anderson et al., 1986)
Approximate Location (after Anderson et al., 1986)
Known BFF Range (after Hall, 1981)

even after extensive search efforts were expended. The probability of this occurring was deemed sufficiently small that the benefits of selective sampling outweighed the risks.

Results — Five areas were ranked and received intensive BFF searches:

1. *Ekalaka area; Carter County; southeast Montana*

Ten possible BFF sightings, including one made by a MFWP employee in 1977, and two museum specimens were reported from the Ekalaka area. Search efforts consisted of 38 person days of diurnal winter and nocturnal summer BFF searches on about 4,500 acres (1,821 ha) of prairie dog colonies. These efforts resulted in the discovery of one cranium and two mandibles from 2 individual BFFs on the same colony where the 1977 sighting was made. This skeletal material was found on one burrow mound in a portion of the colony which had been repeatedly subjected to prairie dog poisoning and shooting. No other BFF sign was found. In addition to these efforts, extensive and intensive surveys were conducted by several USFWS crews between 1983 and 1988. It was concluded that BFFs were recent residents of the area, but for some unknown reason were no longer present.

2. *Charles M. Russell National Wildlife Refuge (CMR); Phillips, Valley, and Garfield Counties; northcentral Montana*

Four BFF reports of varying veracity were reported from CMR in past years. Search efforts consisted of 24 person days of summer nocturnal and winter diurnal searches on about 5,000 ac (2,024 ha) of colonies. No evidence of BFF presence was observed.

3. *Fort Belknap Indian Reservation; Phillips and Blaine Counties; northcentral Montana*

Three unconfirmed BFF sightings and 1 BFF skull are reported from Fort Belknap. Search efforts (summer nocturnal and winter diurnal surveys) totalled 46 person days on over 15,000 ac (6,070 ha) of prairie dog colonies. No evidence indicating BFF presence was discovered. Additional searches conducted by the USFWS and the BIA on Fort Belknap had similar results.

4. *BLM and Private lands; Phillips County; northcentral Montana*

At least 6 unconfirmed BFF sightings and two museum specimens are reported from southern Phillips County. Very accurate data on prairie dog distributions, activity, and history in this area were collected by J. Grensten, Phillips Resource Area of the BLM. Search efforts totalled 34 person days on over 5,000 ac (2,023 ha) of prairie dog colonies. In addition, numerous intensive BFF searches were conducted by BLM personnel and others in the same general area. BFFs or their sign were not observed during this or other search efforts.

5. *BLM and Private lands; Miles City area; Custer and Prairie Counties; southeast Montana*

Three unconfirmed BFF sightings and 3 museum specimens are reported from this area. Accurate prairie dog distribution and activity data were available from the Miles City Office of the BLM and from additional colony location surveys. Efforts totalled 28 person days on nearly 5,000 ac (2,023 ha) of prairie dogs with no evidence of BFFs discovered.

6. *Additional short-term searches, statewide*

Numerous short-term intensive BFF searches were conducted on prairie dog colonies and complexes throughout the eastern two-thirds of the state during winter and summer. These efforts totalled 50 person days on about 7,000 ac (2,833 ha) of prairie dogs. No evidence of BFF presence was found.

CONCLUSIONS

Although no BFF populations were discovered, much useful information regarding the extent of prairie dog ecosystems in Montana has been collected. The Reward Program, designed to increase the volume of BFF reports made to appropriate agencies, was successful and continues to generate new reports. This program should remain in effect until recovery efforts, involving the reintroduction of BFFs into the wild, begin. BFF reports should continue to be evaluated and follow-up efforts made of good reports. Land managers may find the wealth of information regarding prairie dog distributions in Montana particularly relevant and helpful in developing management plans which conserve the ecologically important prairie dog ecosystem and provide critical habitat for species which are dependent upon this ecosystem.

ACKNOWLEDGMENTS

The financial, technical, and administrative support of this project by the Montana Department of Fish, Wildlife, and Parks Department and the U.S. Fish and Wildlife Service through the Endangered Species Act Section 6 Program is greatly appreciated. The cooperation of these agencies, and the Bureau of Land Management, U.S. Forest Service, Bureau of Indian Affairs, Indian Reservations, U.S. Fish and Wildlife Service-Refuge Program, Montana Department of Agriculture, and the Northern Rockies Conservation Cooperative was essential to successful completion of this work. Field and office assistance from A. Dood, J. Cada, D. Flath, T.W. Clark, R. Crete, S. Forrest, J. Grensten, D. Bricco, M. Gorges, G. Smitman, D. Smith, A. Beach, D. Casey, and R. Askins is particularly appreciated. D. Casey and T.W. Clark provided valuable comments on the manuscript.

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APPENDIX 1

Standardized Black-footed Ferret Report Form

$5000 REWARD

FOR INFORMATION OR A PHOTO WHICH RESULTS IN THE VERIFICATION OF ONE OR MORE LIVE BLACK-FOOTED FERRETS IN MONTANA

ELIGIBILITY:

To be eligible for the reward, a person must provide all the information required on the black-footed ferret report form on the back of this sheet. Payment of the reward is contingent on confirmation of one or more live wild black-footed ferrets in Montana. Employees of cooperating agencies listed below are ineligible for receiving the reward.

CONDITIONS:

1. The evidence must be obtained legally.
2. Permission to trespass on private lands must have been granted by the landowner or his agent.
3. When the Montana Department of Fish, Wildlife and Parks follows up on a report, the person who made the report must assist with the verification.
4. The Montana Department of Fish, Wildlife and Parks reserves the right to follow up only those reports which, by their criteria, provide the best details and substantive documentation of black-footed ferret occurrence in Montana.
5. The black-footed ferret is protected by both state and federal laws and must not be harassed, trapped, or killed.
6. This reward offer expires October 1, 1988.

RECOMMENDATIONS:

1. Do not attempt to catch, detain, or harass a black-footed ferret. Such activities violate both state and federal laws.
2. Take a photograph, if possible. All reports will be systematically evaluated, and only those ranked relatively high will be followed up.
3. Make your report immediately.
4. Handouts on survey and identification techniques are available from any of the seven Department regional headquarters and at most Bureau of Land Management offices. A black-footed ferret survey training video is also available at the same locations.

Sponsored by Wildlife Conservation International, a division of the New York Zoological Society

Administered by the Montana Department of Fish, Wildlife and Parks, in cooperation with the Bureau of Land Management, U.S. Fish and Wildlife Service, U.S. Forest Service, Bureau of Indian Affairs, and the Montana Department of Agriculture

GOOD LUCK!

FOLD HERE

Photos by Dave Brown

FOLD HERE

Return Address

_____

_____

_____

Place
Stamp
Here

Ferret Search
Montana Department of Fish, Wildlife and Parks
Montana State University, Box 5
Bozeman, Montana 59717

BLACK-FOOTED FERRET REPORT FORM:

Note: Since this report will be of value to you and our department only if what you have seen is a black-footed ferret, we encourage you to make the report only after you have obtained very convincing evidence that a ferret was observed. Since we will get many reports, only the few best reports will be followed up for verifications. The most complete evidence you can provide will be a clear photograph of the animal and a precise location.

1. What time of day did you observe the animal(s)? _____(am-pm)
   What was the date of the observation? Month _____Day _____
2. Number of animals seen _____.
3. Did you use binoculars or telescope _____?
   If so, what was the magnification and size (eg. 7 x 35)?
   _____
4. Did you take any photographs? _____
   If so, are copies enclosed? _____
5. Where did you make this observation? (Be specific- draw a map & include distance & directions): _____
   _____
   _____
   Include: Range _____Township_____ and Section _____if you can.
6. Describe the animal(s) in detail:
   Coloration (head, tail, body, etc.):_____
   _____
   _____
   Size: _____
   _____
   Activity (walking, running, standing, etc.):_____
   _____

Note: It is helpful to make comparisons with other animals or things which are common, for example "it was the color of a siamese cat".

7. What was the closest distance between you and the animal(s) when you made the observation _____
8. How long did you observe the animal(s): _____
9. If other people saw the animal with you (or later), please list their names and phone numbers.

Name	Phone Number
_____	_____
_____	_____
_____	_____

10. Was this animal on or near a prairie dog town?_____
    If near, how close was the animal(s) to the prairie dog town?_____
    How big (approximate acres) was the prairie dog town?_____
11. If asked, would you be willing to show a member of the ferret search team the location of this sighting? _____
12. Additional comments: _____
    _____
    _____

13. Reported by:
    Name: _____ Phone: _____
    Address: _____
    City: _____ State _____ Zip _____

14. Observed by: (Fill in "same" if same as above)
    Name: _____ Phone: _____
    Address: _____
    City: _____ State _____ Zip _____

Take or Mail this report to **Ferret Search, Montana Department of Fish, Wildlife & Parks, Box 5, Montana State University, Bozeman, Montana 59717,** or call 994-3285, or 587-0597 after hours, for more information.

Note: This form can be used as a mailer by folding it on the dotted lines on the reverse side. If a picture is enclosed tape, the mailer edges to prevent loss of photo.

APPENDIX 2

Black-footed Ferret Report Evaluation Form

PROCEDURE TO FOLLOW UP FERRET REPORTS AND/OR VERIFIED SIGHTINGS

The purpose of this procedure is to establish a formal chain of events so that each party's responsibility is well defined, resulting in a speedy and smooth course of action.

1. The MDFWP will act as a central clearing house for all ferret reports/sightings and will initiate the response procedure when ferret report/sightings have been made.

2. All ferret reports/sightings should be transferred to the MDFWP research office in Bozeman within eight hours of receipt. Reports should be given to the following people in order of priority:

Name	*Office Number*	*Home Number*
Arnold Dood	994-6433	586-7237
John Cada	994-6363	587-0597
Dennis Flath	994-6354	587-0866
Margaret Morelli	994-3285	586-5559

During non-office hours, these individuals should be contacted at their residences.

3. To expedite transfer of report information within each agency, it is recommended that the first individual obtaining the information contact the MDFWP directly.

4. Information to obtain and report should include as a minimum the following:

a. Name, address and telephone number of the observer (and person reporting);
b. Complete description of location of observation as well as geographical location (township, range, section);
c. Date and time of observation;
d. Number of animals observed;
e. Distance to animal(s) observed in feet;
f. Length of time observed;
g. Activity of animal(s);
h. Distance to and size of nearest prairie dog community;
i. Circumstances of observation.

5. One or more of the following individuals will evaluate the validity of the report: Arnold Dood, Dennis Flath, John Cada, Ron Crete, Tim Clark, and Tom Campbell. The report will be scored based on the following criteria:

a. Adequacy of photograph. Likely ferret = 10 pts.; possible = 5 pts.; and no picture or not ferret = 0 pts.;

b. Location. On prairie dog town and other prairie dog towns within 3 mi. = 10 pts.; on or near prairie dog town and no other towns within 3 mi. = 5 pts.; no prairie dog towns in vicinity = 0 pts.;

c. Distance of observation. Within 50 yards or 200 yds through 4+ power telescope = 10 pts.; within 50-100 yds or 200 to 400 yds through 4+ power scope = 5 pts.; over 100 yds or 400+ yds through 4+ power scope = 0 pts.;

d. Length of time observed. 5 or more min. = 10 pts.; 30 seconds to 5 min. = 5 pts.; less than 30 seconds = 0 pts.;

e. Description of animal. Mask = 5 pts.; size = 1 pt.; tail length and color = 1 pt.; body color = 1 pt.; and leg color = 2 pts.;

f. Behavior (bonus points). 5 pts. if ferret behavior described;

g. Observer reliability (bonus points). 5 pts. if experienced observer.

The following categories would be determined based upon the above scoring system:

a. Highly probable. 40-50 pts. with no zeros on any item. Action: Followup recommended without delay;

b. Likely. 30-40 pts. with no zeros or 40-50 pts. with one zero. Action: Followup within seven days;

c. Fair. 22-30 pts. with no zeros or 30-40 pts. with one zero. Action: Followup if convenient or if other reports have come from same vicinity;

d. Unlikely. All other point categories. Action: No action recommended.

7. If a followup is planned, the USFWS, MDFWP, and Biota will be notified immediately and a decision made as to the follow up search procedure. If no followup is planned, the information will be forwarded to the above parties by mail.

8. A followup search in response to a report will be as follows:

   a. One to three (maximum) of the involved researchers will contact private landowners in the vicinity of the search and inform them of our desire to follow up and solicit their support;

   b. Up to four field biologists will begin prearranged surveys;

   c. The length of time spent in the area surveying will be dependent upon the judgement of the field researchers.

9. When a ferret sighting has been made, immediate confidentiality will be maintained and the following actions will be taken:

   a. The USFWS will be notified, consulted, and impending procedure will be agreed upon;

   b. The landowner/lessee or public agency landowner will be contacted by MDFWP within 48 hours, if possible, to work out details of the follow up effort;

   c. A low-key assessment of the black-footed ferret population will be conducted by a minimum number of field biologists and will continue for approximately 90 days;

   d. After four to six days the cooperating agencies will be notified of the preliminary status of the sighting;

   e. Public meetings and news releases will be coordinated by the MDFWP in cooperation with MDA within 14 to 21 days after verification has been made;

   f. If a population of ferrets is found, meetings with affected landowners and cooperating agencies will be held to develop an interim management plan for each land ownership; and

   g. After 120 to 180 days a general plan with action goals for black-footed ferret conservation and recovery will be developed.

Attributes of Black-tailed Prairie Dog Colonies in Northcentral Montana, with Management Recommendations for the Conservation of Biodiversity

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Abstract.—Black-tailed prairie dog (BTPD; *Cynomys ludovicianus*) colony dynamics and associated vertebrate species were studied in Phillips County, Montana in 1981, 1984, and 1988. Average colony size increased, whereas mean expansion rate decreased. Colony size was related to colony expansion rate. Smaller colonies expanded at faster rates than larger colonies, but this difference was greater from 1981-1984 than from 1984-1988. Expansion rate was not related to nearest colony distance, nor to the number or area of surrounding colonies. Burrow opening density was not related to colony size, but was related to the distance to the nearest colony and to the number and area of surrounding colonies. These findings are discussed in relation to a logistic model of colony growth, physical barriers, recreational prairie dog hunting, and human disturbances. In 1988 70 bird species, 12 mammal species, and 1 reptile species were found associated with prairie dog colonies. Of these, 30 birds and 1 mammal were previously unreported in association with BTPDs. Colony size and number of colonies within 4 mi (6.4 km) of a colony accounted for 47.6 of the variation in bird species richness associated with each colony. These findings were consistent with island biogeographic theory. Management of BTPD colonies for the conservation of biodiversity is discussed in relation to our findings and theories of insular biology.

Black-tailed prairie dog (BTPD; *Cynomys ludovicianus*) colonies are distinct and important biotic communities in the mid- to short-grass prairies and desert grasslands of North America (Whicker and Detling 1988). These communities and their physical environment comprise what has been referred to as the prairie dog ecosystem (Montana Black-footed Ferret Working Group 1988). The relationships between community members are complex and largely unexamined (Clark 1986). One of the primary goals in the management of prairie dog ecosystems should be the maintenance of biological diversity. To further that objective, we examined BTPD colony attributes and associated species richness.

The value of both ecological and genetic diversity is increasingly emphasized for a variety of reasons (Fisher et al. 1969, Myers 1979, Terborgh 1979, Wilson 1986). Ecological diversity has been associated with ecosystem stability and, while the loss of a single species may not produce obvious detrimental effects, grave consequences including ecosystem collapse are possible especially with the loss of "keystone" species (Slobodkin and Sanders 1969, Pimm 1986). Genetic diversity provides the source of innumerable agricultural, medicinal, and industrial products and enables species to adapt and evolve in the face of environmental changes (Ehrlich et al. 1977, Wilson 1986).

BTPDs create a habitat mosaic relative to adjacent communities that can be beneficial to other species. Colony boundaries are characterized by abrupt vegetation change (Koford 1958, Knowles 1982). Prairie dogs burrow extensively, clip tall vegetation, and forage on perferred plant species (Osborn 1942, Koford 1958, Archer et al. 1987). The result is a habitat characterized by decreased vegetative height and cover, and increased bare ground, soil movement, and vegetative diversity compared with surrounding areas. Grasses and shrubs are usually reduced, while forbs generally increase (Koford 1958, Knowles 1982, Knowles et al. 1982, Olson 1985). Population and burrow-opening densities are usually correlated (Houston et al. 1986). Both vary considerably, the former reportedly ranging from as few as 1-2/ac (2-4/ha) to as many as 33.4/ac (82.6/ha) for a young, rapidly expanding colony (King 1955, Koford 1958, Smith 1958, Tileston and Lechleitner 1966, Sheets et al. 1971, Garret 1982, Knowles 1982, Archer et al. 1987, Clark et al.1987). For a further review of prairie dog literature see Clark (1986).

This paper characterizes BTPD colony dynamics and vertebrate species associations in Phillips County, Montana over an eight year period (1981-1988). The factors influencing colony expansion and numbers of avian species associated with prairie dog colonies are analyzed.

STUDY AREA

This study was conducted in the Bureau of Land Management's (BLM) Phillips Resource Area (Phillips RA),

located in northcentral Montana (Figure 1). It encompasses 2.9 million acres (1.17 million ha), 1.3 million acres (0.52 million ha) of which are under Federal ownership. The topography varies from flat upland plains and rolling hills to badlands, rough breaks, and mountains. Elevation varies from 2,500-5,500 ft (750-1650 m). Soils are derived from glacial till, sedimentary bedrock, and alluvium from mixed rock sources, resulting in complex and diverse soil patterns (U.S.D.I., BLM 1982). Climate is continental with mean annual precipitation of 11-13 in (28-33 cm) and temperature of -40 to 100 °F (-40 to 38 °C; Clark et al. 1987). Grasslands typical of the Northern Great Plains dominate the area, but sagebrush (*Artemisia* spp.) and greasewood (*Sarcobatus vermiculatus*) are common. Major grasses include needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), Sandberg bluegrass (*Poa sandbergii*), and green needlegrass (*Stipa viridula*). Human population density is about 1 person per mi² (0.4 persons per km²). Cattle ranching and grain farming represent the major land uses. For a more complete description see U.S.D.I., BLM (1982).

Prairie dog management in Phillips RA includes both poisoning and recreational shooting. A prairie dog management plan was prepared in 1982 which emphasized poisoning (U.S.D.I., BLM 1982); however, personnel and money constraints forced plan modification. The plan currently aims at encouraging recreational prairie dog shooting by providing hunters with information letters and maps of prairie dog colonies and posting (marked with signs to guide recreationalists) larger colonies. Large scale shooting began in 1984. Although all colonies on public lands are open to hunting, only colonies over 50 ac (22 ha) are posted.

METHODS

Data collection was initiated in the absence of hypotheses and procedures were not established to conform to research design. Any *post hoc* hypotheses would consequently be artificial, therefore none were attempted. Since hypotheses were not being tested, statistical descriptions are intended to illustrate trends, not statistical inference. We do not report inferential test statistics (e.g., *F* values) because such values might infer a precision which was not present in this study.

BTPD colonies were studied during the summers of 1981, 1984 , and 1988. Field work for 1981 and 1984 was completed prior to the onset of large scale prairie dog shooting. In 1981, colonies were mapped from aerial photographs, whereas in 1984 and 1988, colonies were mapped on 7.5 minute USGS topographic maps. We (JG and RR) mapped 92 colonies in 1981, an additional 57 colonies (149 colonies total) in 1984, and an additional 21 colonies (170 colonies total) in 1988. Most of the additional 78 (57 + 21) colonies examined were not new colonies, but ones which expanded from private or state land onto federal property. Colony area was determined to the nearest 0.1 ac (0.04 ha) using an electronic planimeter. Expansion rates were calculated to compound size increases yearly using the formula:

$$\left(\sqrt[x-y]{(size_x/size_y)} \right)^{-1}$$

where x = the most recent year sampled and y = the previous year sampled.

Additional data were collected on the 170 colonies mapped in 1988: (1)burrow density, calculated from counts obtained by walking perpendicular transects across the widest portion of each colony and counting all burrow-openings falling within armspan; (2) distance to a colony's nearest neighbor; (3) the number of colonies within 4 mi (6.4 km) of its perimeter; and (4) the area of colonies within 4 mi (6.4 km). A distance of 4 mi (6.4 km) was selected because it approximates the common daily movement distances of black-footed ferrets (*Mustela nigripes*), an important member of the prairie dog ecosystem (Forrest et al. 1985, Richardson et al. 1987, Biggins et al. 1985, 1988).

Colonies examined in 1988 were also surveyed for associated vertebrate species. Each colony was surveyed once by one to three observers. Surveys were conducted during daylight hours, beginning shortly after sunrise and continuing until early evening, but not all colonies were surveyed during the same time of day. Surveys were not performed in temperatures over 95 °F (35 °C) or in rainy weather. The length of time spent on each colony varied with colony size and the number of animals observed, but was generally 1 - 4 hours.

Associated species surveys were conducted by driving across each colony at approximately 75 ft (23 m) intervals. All vertebrates sighted on or foraging over colonies were recorded. If a bird appeared to be nesting further observations were made. Species sighted while walking transects and mapping colonies were also recorded. Although recorded, waterbirds (e.g., Anseriformes, Podicipediformes, Pelecaniformes) were considered to be associated with reservoirs rather than with prairie dog colonies and were therefore not included in the analyses.

Data were analyzed using a SYSTAT statistical package (Wilkinson 1988). Variables were examined for kurtosis and skewness to check for normality. Three variables; colony size, distance to nearest neighbor, and avian species richness, warranted natural log transformations. Parametric statistical analyses were used to compare variables over time, to examine correlations between variables, and to test the significance of linear and multiple regressions. Statistical significance was considered as $P \leq 0.05$.

RESULTS

Results cover two major areas: BTPD colony dynamics and vertebrate species associations. The former addresses colony size, expansion, and population, whereas the latter focuses on colony attributes relating to the number of associated vertebrate species present.

Prairie Dog Colony Dynamics

The average size of 92 BTPD colonies increased significantly from 93.4 ac (37.8 ha) in 1981 to 135.4 ac (54.8 ha) in 1984 (Wilcoxon rank sum = 6.8, $P<0.001$) and from 135.4 ac (54.8 ha) in 1984 to 153.4 ac (62.1 ha) in 1988 (Wilcoxon rank sum = 3.0, $P<0.01$; Figure 2). Mean colony expansion rate decreased significantly between the 1981-1984 and the 1984-1988 intervals (Wilcoxon rank sum = -5.5, $P< 0.001$; Figure 2).

Colonies generally expanded over the entire 8 years. Of 92 colonies, 77 (84 percent) showed increases during both the 1981-1984 and the 1984-1988 intervals, three (3 percent) remained unchanged, two (2 percent) decreased during both intervals, and the remaining 10 (11 percent) colonies decreased from 1981-1984, but then remained constant until 1988. No colony increased during one time interval and decreased during the other.

Figure 1.—Map of Phillips Resource Area in northcentral Montana.

Bureau of Land Management
Phillips Resource Area, Montana

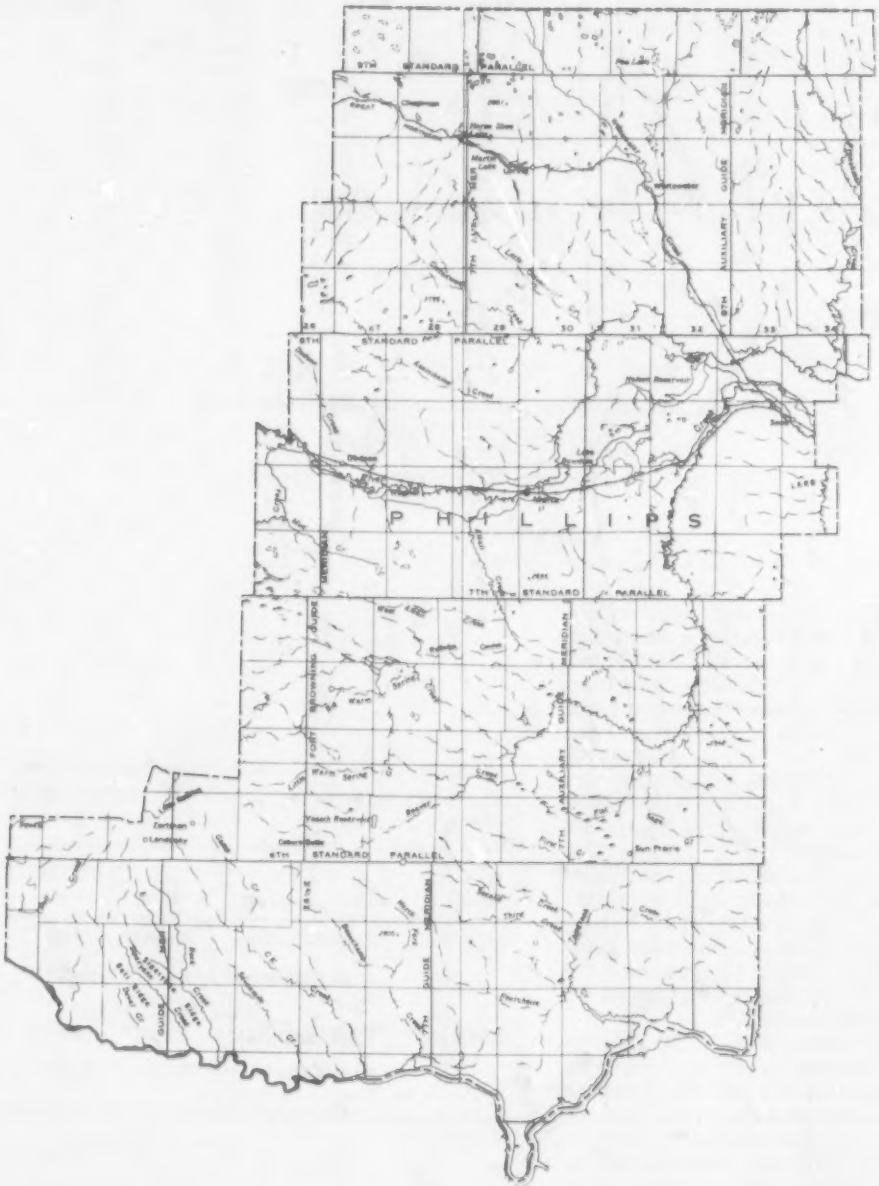
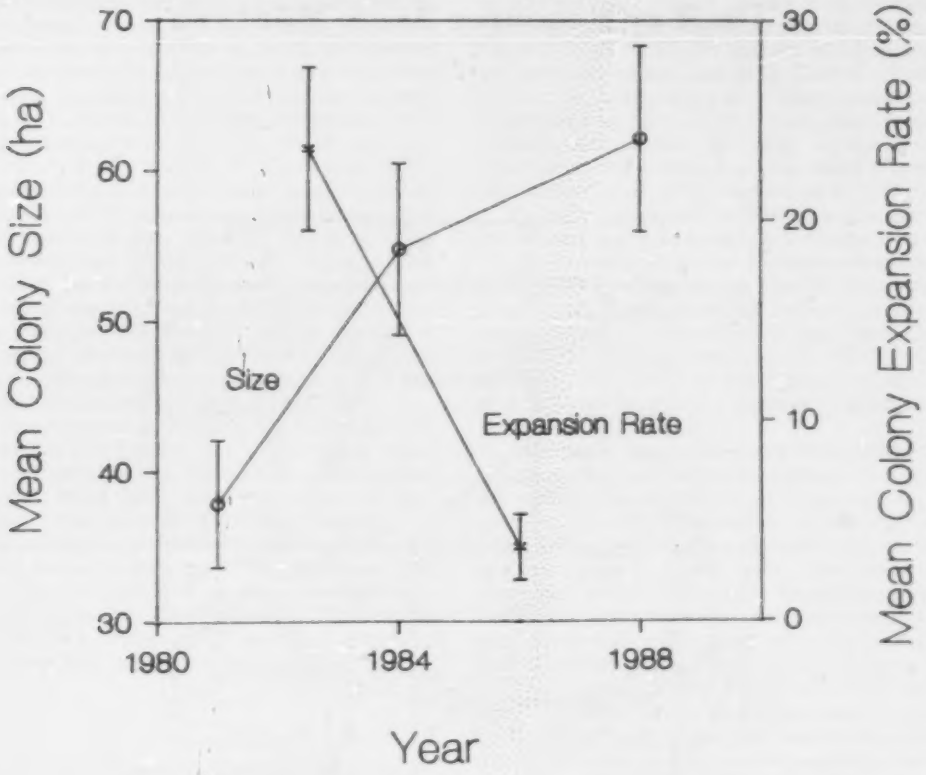


Figure 2.—Colony size and expansion rate trends for 92 BTPD colonies in Phillips County, MT. Expansion data represent the 1981-1984 and 1985-1988 intervals. Bars represent standard errors.



Colony size was inversely correlated with colony expansion rates (Figure 3). Smaller colonies expanded at significantly faster rates than larger colonies. From 1981-1984, however, colonies expanded significantly faster than from 1984-1988. The slope of the expansion rate-colony size regression (Figure 3) was significantly greater for 1981-1984 compared with 1984-1988 ($P<0.001$, by ANCOVA). Initial colony size showed a significant negative correlation with expansion rate for both 1981-1984 and 1984-1988, and a positive correlation with area expanded/year for 1981-1984 (Figure 3, Table 1). By the end of the expansion interval, however, colony size was positively correlated with expansion rate for 1984-1988 and with area expanded/year for both 1981-1984 and 1984-1988 (Table 1). Burrow density was not significantly related to colony size (Table 2, Figure 4), and averaged 44.0 ± 1.3 S.E. burrows/ac (108.8 ± 3.3 S.E. burrows/ha) for 170 colonies in 1988 (range=5.5-99.7 burrows/ac, 13.6-246.9 burrows/ha).

Three characteristics of surrounding BTPD colonies were measured; distance to nearest neighbor, and number and area of colonies within 4 mi (6.4 km). We found no significant relationship between these variables and colony expansion rate or area expanded/year for the 149 colonies measured in 1984 and 1988 (Table 2). However, burrow density was significantly correlated with all three variables: positively with distance to a colony's nearest neighbor, negatively with the number of colonies, and negatively with area of colonies within 4 mi (6.4 km) of the colony (Table 2).

Table 1.—Pearson's Correlation Coefficients for 1981-1988 size and expansion characteristics for 92 black-tailed prairie dog colonies

Period	Colony Characteristics	Ln Colony Size 1981	1984	1988
1981-1984	Expansion Rate	-0.586**	-0.062	0.030
	Area Expanded/ Year	0.368**	0.672**	0.595**
1984-1988	Expansion Rate	-0.301**	-0.283**	0.308**
	Area Expanded/ Year	-0.003	-0.029	0.342**

**$P<0.001$

Figure 3.—The relationship expansion rate (%) and colony size (acres)— for 92 BTPD colonies in Phillips County, MT from 1981-1984 (A) and 1984-1988 (B). The linear regressions are significant: (A) R=0.59, P<0.001, (B) R=0.28, P<0.01.

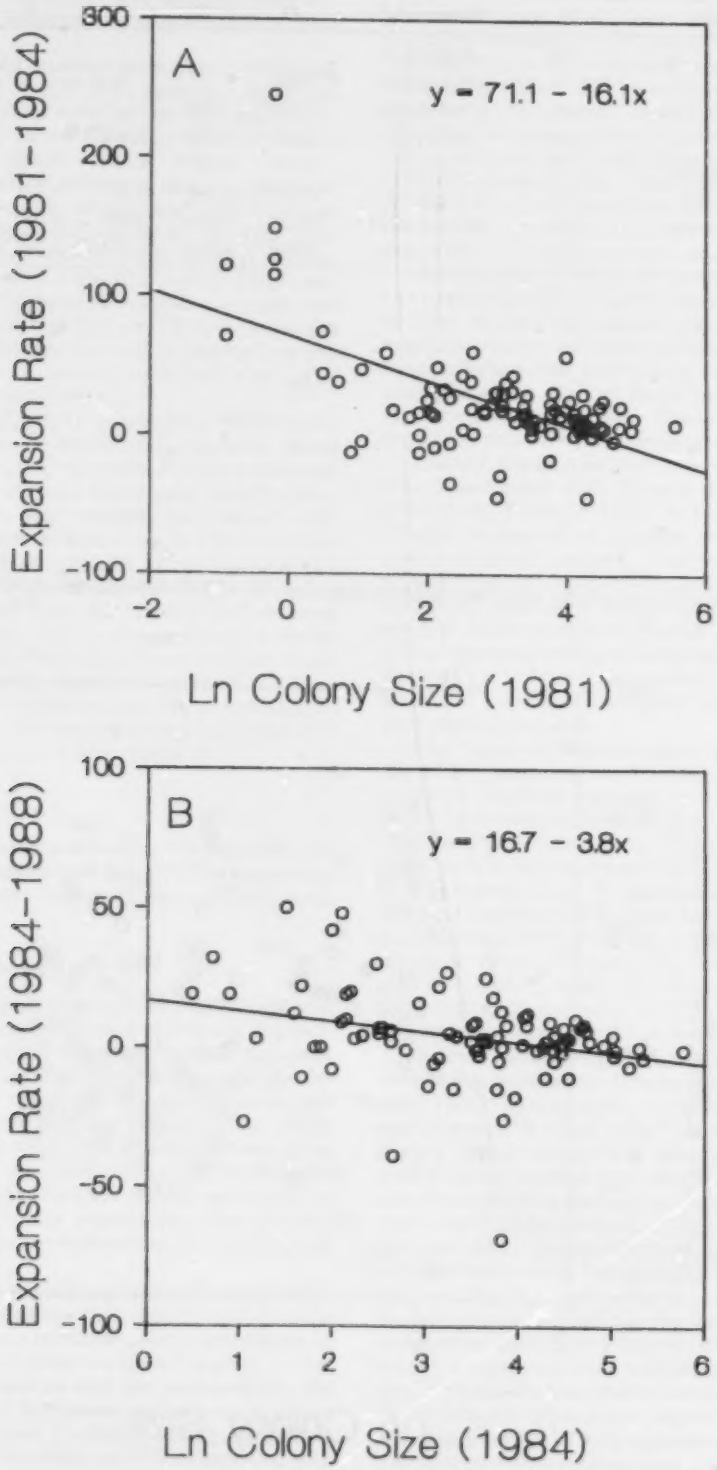
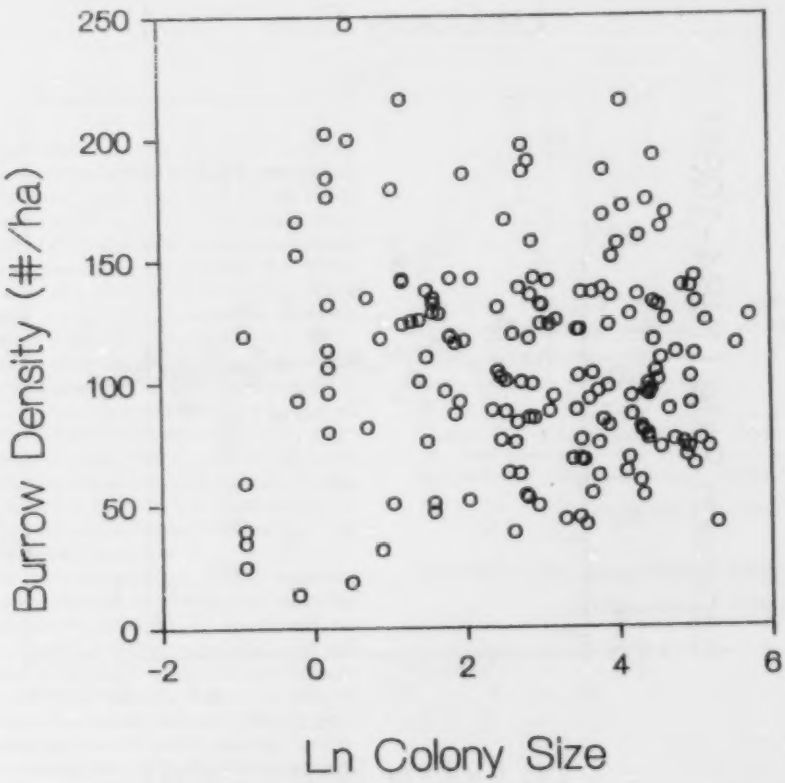


Table 2.—Descriptive statistics and Pearson's Correlation Coefficient for prairie dog colony characteristics in 1988

Colony Characteristics	*N*	Mean (±S.E.)	Colony Characteristics						
			1	2	3	4	5	6	7
1. Ln Size	170	44.6 (±4.1)							
2. Burrow Density	170	108.8 (±3.3)	-0.029						
3. Expansion Rate	149	3.6 (±1.4)	0.268**	0.049					
4. Area Expanded/Year	149	5.5 (±2.1)	0.331**	0.076	0.502**				
5. Ln Dist. to Nearest Neighbor	170	1.7 (±0.1)	-0.109	0.154*	-0.056	0.030			
6. No. Colonies Within 6.4 km	170	9.1 (±0.4)	0.167*	-0.346**	0.127	0.151	-0.325**		
7. Area Colonies Within 6.4 km	170	417.5 (±25.5)	0.139	-0.339**	0.069	0.085	-0.296**	0.874**	
8. Ln Avian Species Richness	170	6.7 (±0.3)	0.660**	-0.029	0.231**	0.242**	-0.093	0.285**	0.274**

*$P<0.05$
**$P<0.01$

Figure 4.—Burrow density vs. colony size (ha) relationship for 170 BTPD colonies in Phillips County, MT. No linear relationship exists ($P=0.71$).



Species Associated With Prairie Dog Colonies

We sighted 83 vertebrate species on or foraging over BTPD colonies, including 70 birds, 12 mammals, and one reptile (Appendix I). We found 30 avian and one mammalian species previously unreported in association with BTPD colonies.

Relatively few mammal species were found on prairie dog colonies (Mean=0.64 ± 0.06 S.E. species/colony), so bird and mammal analyses were performed separately. The log-log species area curve for mammals was linear with a slope of 0.10 ($P<0.001$).

Figure 5A shows the effect of colony size on avian species richness. As expected, avian species richness increased significantly with increasing colony size. Species richness also increased significantly with increasing area of colonies within 4 mi (6.4 km; Figure 5B). There was no significant relationship between species richness and burrow density of each colony (Figure 5C). Avian species richness was also significantly related to prairie dog colony expansion rate, area expanded/year, and number of colonies within 4 mi (6.4 km; Table 2).

To examine further the factors affecting BTPD colony/avian species richness, we performed a stepwise linear regression using all measured variables. Colony size and area of colonies within 4 mi (6.4 km) entered into the stepwise regression. Colony size entered the model first (R^2=0.439). Area of colonies within 4 mi (6.4 km) entered second and, together with colony size, accounted for 47.6 percent of the variance in avian species richness. All other variables were eliminated from the model. Correlations between the expansion rate, area expanded/year, number of colonies within 4 mi (6.4 km) of a colony and its avian species richness are probably explained by direct relationships between a colony's expansion rate, the area it expanded/year, and its size and between number of colonies and area of colonies within 4 mi (6.4 km) (Table 2).

DISCUSSION

The study results are discussed below with respect to the various aspects and relationships of the BTPD ecosystem. Recommendations are made for future research and management.

Prairie Dog Colony Dynamics

Average BTPD colony size increased from 1981 to 1988, while average colony expansion rate decreased (Figure 2). Analysis of the relationship between colony size and expansion rate explains this. From 1981-1984 smaller colonies expanded at higher rates than larger colonies, but larger colonies added more area per colony. From 1984-1988 smaller colonies still expanded at greater rates than larger colonies, but larger colonies no longer added significantly more area per colony than did smaller colonies. In addition, colonies with greater expansion rates became larger than colonies with lower expansion rates by the end of the study.

These findings, and those by Knowles (1982), agree with Garret et al.'s (1982) suggestion that colony populations exhibit logistic growth. As a colony's population grows, it expands in size. Initially, colonies expand rapidly in the presence of abundant resources and low competition. As colonies grow competition increases and resource abundance decreases. Garret and Franklin (1988) suggested that one primary driving force behind BTPD dispersal was a reduction in preferred colony edge vegetation. However, at least two other factors probably forced a reduction in colony growth rates encouraging extracolonial dispersal in our study.

First, physical barriers (e.g., steep slopes or tall, dense vegetation) can slow larger colony expansion. In small colonies, dispersal to the colony's periphery permits rapid expansion into the surrounding prairie and greater access to edge vegetation. But as colonies grow, physical barriers may limit the amount of available, uncolonized prairie. Dispersal in these larger colonies might occur extracolonially, because intracolonial dispersal might result in reduced access to edge vegetation. Future studies should examine how low vegetation height and density, poor soil productivity, and physical barriers affect BTPD dispersal and colony expansion rates.

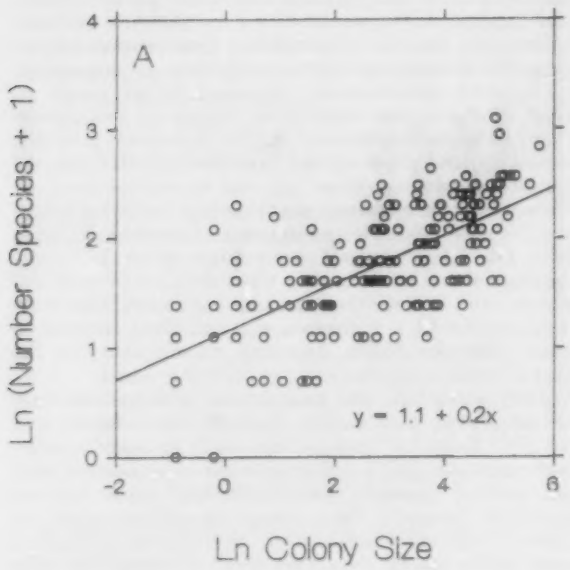
Second, the BLM prairie dog shooting program might have affected BTPD colony expansion. Shooting, starting in 1984, might have caused some of the decline in colony expansion rates. Unfortunately there are no data on BTPD numbers shot, but prairie dog shooting might effectively control prairie dogs if there are a sufficient number of hunters (Knowles 1988). Research should examine the impact of recreational hunting on BTPD colonies.

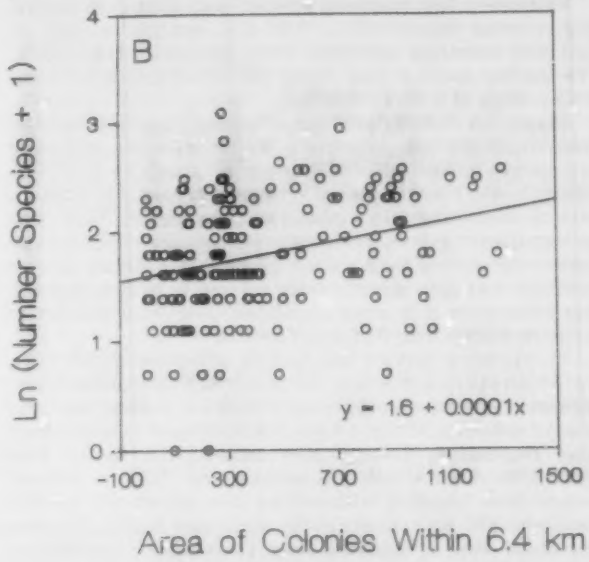
Colony expansion and new colony establishment are often associated with human disturbances (Osborn and Allan 1949, Knowles 1982). In this study we found a large, though unquantified, number of colonies associated with cattle salting grounds, reservoirs, and other regions affected by humans. Such areas are characterized by decreased vegetative height and density, often a result of intense cattle traffic (Knowles 1986). Grazing practices offer a potentially important prairie dog management tool. Research should compare effects of livestock grazing with effects of increased livestock traffic on colony establishment and expansion.

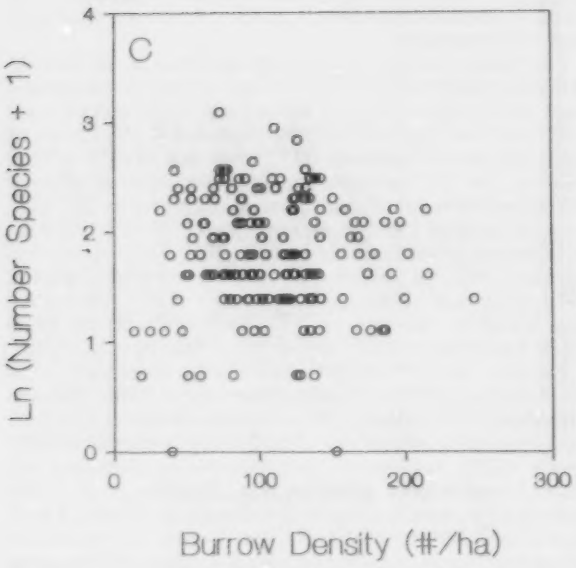
The range of burrow-opening densities in this study (13.6-246.9 burrows/ha, 5.5-99.7 burrows/ac) is within the range of densities reported elsewhere (6-116 burrows/ac, 15-287 burrows/ha; Koford 1958, Archer et al. 1987). Koford (1958) suggested that most BTPD colonies have 20-40 burrows/ac (50-100 burrows/ha). Various studies showed BTPD densities as: 25 burrows/ac (62 burrows/ha; Cottom and Caroline 1965), 34-64 burrows/ac (85-158 burrows/ha; Merriam 1902), 41-42 burrows/ac (101-104 burrows/ha; Knowles 1982), 42 burrows/ac (104 burrows/ha; Tileston and Lechleitner 1966), 51 burrows/ac (125 burrows/ha; King 1955), 55 burrows/ac (136 burrows/ha;Smith 1953) and 69 burrows/ac (169 burrow/ha; O'Meilia et al. 1982).

Burrow density may be positively correlated with prairie dog population density (Forrest et al. 1985, Houston et al. 1986). In this study, burrow density was not significantly related to colony size. This finding is consistent with King's (1955) suggestion that population densities are probably not related to colony size. Houston et al. (1986) noted that burrow density is not always an accurate indicator of population density. Burrow density reflects historical and recent past colony conditions. Also, BTPDs clean out more burrows in the spring than they use (Koford 1958). Burrow density can remain relatively constant even though population density decreases (Knowles 1982). Both population density and burrow density are probably more closely associated with habitat quality than with colony size. Potentially important factors affecting habitat quality include soil type, slope, vegetative cover type, and rainfall. Biggins et al. (1988) suggest using the ratio of active to inactive burrow-openings as a measure of population density.

Figure 5.—The effect of colony size (A), area of colonies within 4 mi. (6.4 km) (B), and burrow density (C) on avian species richness in 1988 for 170 BTPD colonies in Phillips County, MT. We added "1.0" to the number of avian species for computational purposes. Avian species richness-colony relationships: (A) R=0.66, P<0.001, (B) R=0.28, P<0.001, (C) No linear relationship exists (P=0.59).







Colonies are dynamic, responding to a number of interacting biotic and abiotic factors. Future research should examine the effectiveness of the censusing technique suggested by Biggins et al. (1988) for white-tailed prairie dogs (*C. leucurus*) on BTPDs and investigate the influence of physical and biological factors (e.g. slope, topography, soils, and vegetative cover) on BTPD colony attributes.

Species Associated With Prairie Dog Colonies

A total of 163 vertebrate species have been sighted on BTPD colonies in this and in five other studies (Koford 1958, Tyler 1968, Campbell and Clark 1981, Clark et al. 1982, Agnew 1983; Appendix I). This includes 10 amphibians, 15 reptiles, 101 birds, and 37 mammals. Most of the previously unreported avian species (19 of 30) seen in this study are probably associated with reservoirs rather than with the colonies (i.e., Anseriformes, Pelecaniformes, Podicipediformes).

BTPD activities increase plant and vertebrate diversity on colonies (Hansen and Gold 1977). Agnew et al. (1986) found significantly higher densities of birds and mammals, and greater avian species richness on prairie dog colonies than on adjacent prairie. Several species prey on prairie dogs (e.g., black-footed ferrets; and golden eagles, *Aquila chrysaetos*), some inhabit unused burrows (e.g., burrowing owls, *Athene cunicularia*; and cottontails, *Sylvilagus* spp.), and still others benefit from the environmental alterations of prairie dogs (e.g., mountain plovers, *Charadrius montanus*; and McCown's longspur, *Calcarius mccownii*). Several authors report preferential ungulate grazing on colonies, especially by bison (*Bison bison*), cattle (*Bos tarsus*), and pronghorn (*Antilocapra americana*; Smith 1958, Coppock et al. 1983, Wydeven and Dahlgren 1985, Krueger 1986, Detling and Whicker 1988). For

arthropods, however, the biomass on pastures grazed by cattle alone was three times greater than on pastures grazed by cattle and prairie dogs (O'Meilia et al. 1982). These studies demonstrate the importance of BTPD colonies to other species and highlight the significance of managing colonies favorable to biodiversity. Future studies should examine the dependency of associated species to BTPD colonies, especially threatened or endangered species or organisms listed as species of special concern by state agencies.

BTPD colonies represent distinct, "island-like" habitat patches (Whicker and Detling 1988). Although the prairie between colonies may not present a formidable barrier to dispersal for some vertebrates associated with BTPD colonies, for other vertebrate species it may. An area with a large number of habitat patches may increase dispersal rates into that area and maintain a larger number of immigrants capable of repopulating individual patches (Askins et al. 1987). Our results support predictions from island biogeographic theory that isolated patches of habitat maintain larger numbers of species with increasing patch size and proximity to sources of immigration (MacArthur and Wilson 1967). The number of bird species sighted on prairie dog colonies was significantly related to colony size and area of colonies within 4 mi (6.4 km), the former being the more important variable (Table 2; Figure 5A, B). Other researchers have obtained similar results for birds species distributions in forest habitat patches (e.g., Howe 1984, Askins et al. 1987).

In this study the relationship between colony size and avian species richness was linear, with a slope of 0.220 (Figure 4A), well within the predicted range for insular habitat patches and true islands. Preston (1962), MacArthur and Wilson (1967), and May (1975) predicted that species richness on islands should increase with island area such that the log-log plot is linear with a slope between 0.15 and 0.35. Similar patterns are suggested for habitat islands (MacArthur and Wilson 1967, Diamond 1984). Alternatively, sample plots and continental habitats are theoretically characterized by linear relationships of 0.12-0.17 (MacArthur and Wilson 1967, Diamond and Mayr 1976).

Unfortunately, we were unable to distinguish between avian species strongly associated with, or dependent on colonies and more casually associated or facultative species. Increased sampling effort with increased colony size could, therefore, account for some or all of the relationship. Blake and Karr (1984), however, obtained a slope of 0.223 for all avian species in Illinois forest patches. Future studies should sample on and off colonies to determine which species are strong or dependent associates.

Eight of the mammal species (80 percent) sighted in this study were sighted on fewer than 9 percent of the BTPD colonies examined. These species are probably not associated with prairie dog colonies, but with colonies as a part of the surrounding mid- to short-grass prairies. The relationship between colony size and mammalian species richness supports this suggestion, being linear with a slope (0.10) more similar to that of sample plots and continental habitats than islands or insular habitats.

Insular biology has important implications for the conservation of biodiversity, especially with respect to the size and shape of reserves (review in Simberloff 1988). Early applications of island biogeography theory to reserve design prescriptions aimed at maximizing species richness led researchers to recommend several reserve design principles (e.g., single large reserves are superior to several small ones, minimization of reserve boundaries relative to reserve area; Diamond 1975, Wilson and Willis 1975). Most of these design principles (other than a single large reserve is superior to a single small one) were subsequently challenged (Simberloff 1988). Using empirical evidence, further analysis of island biogeography theory, and metapopulation (groups of subpopulations characterized by greater movement within groups than between them; Andrewartha and Birth 1954) concepts, several researchers recommended establishing several small reserves characterized by at least minimal migration over one large reserve (Higgs and Usher 1980, Gilpin and Diamond 1980, Goodman 1987). An increase in the number of reserves might also decrease the probability of species extinction due to environmental stochasticity via risk-spreading (Simberloff and Abele 1976, Quinn and Hastings 1987). Although the debate continues, insular biological theory can play a useful role in the conservation of biodiversity on prairie dog colonies.

Conservation management of prairie dogs and their associated species should occur at the ecosystem level. BTPD ecosystems are comprised of colony complexes (clusters of colonies; Minta and Clark 1989) which can be thought of as metapopulations of prairie dogs and their associated fauna (Clark et al. 1987). Results of this study suggest that richness of associated vertebrate species on BTPD colonies increases with colony size and regional colony density. Managers should therefore maintain complexes of relatively large colonies linked by "stepping-stone" colonies for species dispersal. Reserve design and future BTPD management should concentrate on the maintenance of biodiversity on prairie dog complexes. Additional research and management knowledge is needed to achieve this goal.

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APPENDIX I
Vertebrate Species Sighted on BTPD Colonies

Species	References
AMPHIBIANS	
Tiger Salamander *(Ambystoma tigrinum)*	2,4
Plains Spadefoot Toad *(Scaphiopus bombifrons)*	4
Couch's Spadefoot Toad *(Scaphiopus couchi)*	4
Chorus Frog *(Pseudacris triseriata)*	2
Northern Leopard Frog *(Rana pipiens)*	2
Great Plains Narrow-mouthed Frog *(Gastrophryne olivacea)*	4
Western Toad *(Bufo boreas)*	2
Green Toad *(Bufo debilis)*	4
Texas Toad *(Bufo speciosus)*	4
Woodhouse's Toad *(Bufo woodhousei)*	4
REPTILES	
Yellow Mud Turtle *(Kinosternon flavescens)*	4
Ornate Box Turtle *(Terrapene ornata)*	3,4
Lesser Earless Lizard *(Holbrookia maculata)*	3,4
Texas Horned Lizard *(Phrynosoma cornutum)*	3,4
Short-horned Lizard *(Phrynosoma douglassi)*	2
Sagebrush Lizard *(Sceloporus graciosus)*	2,3
Eastern Fence Lizard *(Sceloporus undulatus)*	4
Chihuahua Spotted Whiptail *(Cnemidophorus exanquis)*	3
Texas Spotted Whiptail *(Cnemidophorus qularis)*	4
Little Striped Whiptail *(Cnemidophorus inornatus)*	3
Racerunner *(Cnemidophorus sexlineatus)*	4
Gopher Snake *(Pituophis melanoleucus)*	2,4
Common Garter Snake *(Thamnophis sirtalis)*	2
Western Diamondback Rattler *(Crotalus atrox)*	4,5
Prairie Rattlesnake *(Crotalus viridis)*	1,2,3,4,5
BIRDS	
Eared Grebe *(Podiceps nigricollis)*	1
Pied-billed Grebe *(Podilymbus podiceps)*	1
White Pelican *(Pelecanus erythrorhynchos)*	1
Double-crested Comorant *(Phalacrocorax auritus)*	1
Great Blue Heron *(Ardea herodias)*	1
Black-crowned Night Heron *(Nycticorax nycticorax)*	1
Canada Goose *(Branta canadensis)*	1
Snow Goose *(Chen caerulescens)*	4
Mallard *(Anas platyrhynchos)*	1,6
Gadwall *(Anas streperа)*	1
Northern Pintail *(Anas acuta)*	1,6
Green-winged Teal *(Anas crecca)*	1,2
Blue-winged Teal *(Anas discors)*	1,6
American Widgeon *(Anas americana)*	1
Redhead *(Aythya americana)*	1
Lesser Scaup *(Aythya affinis)*	1
Ruddy Duck *(Oxyura jamaicensis)*	1
Turkey Vulture *(Cathartes aura)*	4,6
Mississippi Kite *(Ictinia mississippiensis)*	4
Sharp-shinned Hawk *(Accipiter striatus)*	1
Red-tailed Hawk *(Buteo jamaicensis)*	2,4,5,6
Swainson's Hawk *(Buteo swainsoni)*	1,2,3,4,6
Rough-legged Hawk *(Buteo lagopus)*	4,5
Ferruginous Hawk *(Buteo regalis)*	1,2,3,4,6
Golden Eagle *(Aquila chrysaetos)*	1,2,4,5
Bald Eagle *(Haliaeetus leucocephalus)*	4
Northern Harrier *(Circus cyaneus)*	1,2,4,5,6
Prairie Falcon *(Falco mexicanus)*	1,2,4,5,6
Merlin *(Falco columbarius)*	1
American Kestrel *(Falco sparverius)*	1,2,3,4,6
Sage Grouse *(Centrocerus urophasianus)*	1,2

Species	References
BIRDS (Cont.)	
Lesser Prairie Chicken *(Tympanuchus pallidicinctus)*	4
Sharp-tailed Grouse *(Tympanuchus phasianellus)*	1,5,6
Northern Bobwhite *(Colinus virginianus)*	4
Scaled Quail *(Callipepla squamata)*	4
Gray Partridge *(Perdix perdix)*	1
Sora *(Porzuna carolina)*	6
American Coot *(Fulica americana)*	1
American Avocet *(Recurvirostra americana)*	1
Killdeer *(Charadrius vociferus)*	1,2,4,6
Mountain Plover *(Charadrius montanus)*	1,2,4
Lesser Golden Plover *(Pluvialis dominica)*	4
Marbled Godwit *(Limosa fedoa)*	1
Long-billed Curlew *(Numenius americanus)*	1,4,6
Upland Sandpiper *(Bartramia longicauda)*	1,4,6
Greater Yellowlegs *(Tringa melanoleuca)*	1
Lesser Yellowlegs *(Tringa flavipes)*	1
Willet *(Catoptrophorus semipalmatus)*	1
Wilson's Phalarope *(Phalaropus tricolor)*	1
Baird's Sandpiper *(Calidris bairdii)*	4
Buff-breasted Sandpiper *(Tryngites subruficollis)*	4
Herring Gull *(Larus argentatus)*	1
California Gull *(Larus californicus)*	1
Ring-billed Gull *(Larus delawarensis)*	1
Rock Dove *(Columba livia)*	4,6
Mourning Dove *(Zenaida macroura)*	1,2,3,4,6
Great Horned Owl *(Bubo virginianus)*	2,6
Burrowing Owl *(Athene cunicularia)*	1,2,3,4,6
Common Nighthawk *(Chordeiles minor)*	1,2,4
Northern Flicker *(Colaptes auratus)*	1,4
Ladder-backed Woodpecker *(Picoides scalaris)*	4
Eastern Kingbird *(Tyrannus tyrannus)*	1,4,6
Western Kingbird *(Tyrannus verticalis)*	1,2,4,6
Scissor-tailed Flycatcher *(Tyrannus forficatus)*	4
Say's Phoebe *(Sayornis saya)*	6
Horned Lark *(Eremophila alpestris)*	1,2,3,4,6
N. Rough-winged Swallow *(Stelgidopteryx serripennis)*	6
Barn Swallow *(Hirundo rustica)*	1,2,4,6
Cliff Swallow *(Hirundo pyrrhonota)*	1,2,4
Black-billed Magpie *(Pica pica)*	1,2
Chihuahuan Raven *(Corvus cryptoleucus)*	4
American Crow *(Corvus brachyrhynchos)*	4,6
Northern Mockingbird *(Mimus polyglottos)*	4
Sage Thrasher *(Oreoscoptes montanus)*	1
Curved-billed Thrasher *(Toxostoma curvirostre)*	3
American Robin *(Turdus migratorius)*	1
Mountain Bluebird *(Sialia currucoides)*	1
Sprague's Pipit *(Anthus spragueii)*	4
Loggerhead Shrike *(Lanius ludovicianus)*	1,2,4,6
European Starling *(Sturnus vulgaris)*	1,4,6
Eastern Meadowlark *(Sturnella magna)*	4
Western Meadowlark *(Sturnella neglecta)*	1,2,3,4,6
Yellow-headed Blackbirds *(Xanthocephalus xanthocephalus)*	1,6
Red-winged Blackbird *(Agelaius phoeniceus)*	1,4,6
Northern Oriole *(Icterus galbula)*	4
Brewer's Blackbird *(Euphagus cyanocephalus)*	1,4
Boat-tailed Grackle *(Quiscalus major)*	4
Common Grackle *(Quiscalus quiscula)*	6
Brown-headed Cowbird *(Molothrus ater)*	1,2,4
Lark Bunting *(Calamospiza melanocorys)*	1,2,4,6
Snow Bunting *(Plectrophenax nimalis)*	2
Savannah Sparrow *(Passerculus sandwichensis)*	1,2,4
Grasshopper Sparrow *(Ammodramus savannarum)*	1,6

Species	References
BIRDS (Cont.)	
Baird's Sparrow *(Ammodramus bairdii)*	1
Vesper Sparrow *(Pooecetes gramineus)*	1,2,4
Lark Sparrow *(Chondestes grammacus)*	1,3,4
Brewer's Sparrow *(Spizella breweri)*	1
McCown's Longspur *(Calcarius mccownii)*	1,2,4
Lapland Longspur *(Calcarius lapponicus)*	4
Chestnut-collared Longspur *(Calcarius ornatus)*	1,2,4,6
House Sparrow *(Passer domesticus)*	4,6
MAMMALS	
Eastern Mole *(Scalopus aquaticus)*	4
Bat *(Myotis spp.)*	2
Black-tailed Jackrabbit *(Lepus californicus)*	3,4,5
White-tailed Jackrabbit *(Lepus townsendii)*	1,2,5
Desert Cottontail *(Sylvilagus auduboni)*	2,3,4,5
Cottontail spp. *(Sylviiagus spp.)*	1
Spotted Ground Squirrel *(Citellus spilosoma)*	4
Thirteen-line Ground Squirrel *(Citellus spilosoma)*	2,3,4,5,6
Least Chipmunk *(Eutamius minimus)*	2
Richardson's Ground Squirrel *(Spermophilus richardsonii)*	1
Plains Pocket Gopher *(Geomys bursarius)*	3,4
Pocket Gopher *(Thomomys spp.)*	2,5
Ord Kangaroo Rat *(Dipodomys ordi)*	3,4,5
Hispid Pocket Mouse *(Perognothus hispidus)*	6
Western Harvest Mouse *(Reithrodontomys megalotis)*	6
Deer Mouse *(Peromyscus maniculatus)*	2,4,5,6
Wyoming Pocket Mouse *(Perognathus fasciatus)*	2
Southern Plains Woodrat *(Neotoma micropus)*	3,4
Northern Grasshopper Mouse *(Onychomys leucogaster)*	2,5,3
Prairie Vole *(Microtus ochrogaster)*	6
House Mouse *(Mus musculus)*	6
Coyote *(Canis latrans)*	1,2,3,4,5
Red Fox *(Vulpes vulpes)*	1,2
Swift Fox *(Vulpes velox)*	4
Raccoon *(Procyon lotor)*	2,4
Long-tailed Weasel *(Mustela frenata)*	2,3
Black-footed Ferret *(Mustela nigripes)*	5
Mink *(Mustela vison)*	2
Striped Skunk *(Mephitis mephitis)*	2,4
Badger *(Taxidea taxus)*	1,2,3,4,5
Bobcat *(Lynx rufus)*	4,5
Domestic Hourse *(Equus cabalis)*	1,2
Elk *(Cervus elaphus)*	1
Mule Deer *(Odoccileus hemionus)*	1,2
Pronghorn *(Artilocapra americana)*	1,2,3,5
Domestic Cattle *(Bos tarsus)*	1,2
Bison *(Bison bison)*	4,5
Domestic Sheep *(Ovis aries)*	1,2

References: 1—This Study
2—Campbell and Clark (1981)
3—Clark et al. (1982)
4—Tyler (1968)
5—Koford (1958)
6—Agnew (1986)

Habitat Suitability Analysis of Potential Translocation Sites For Black-footed Ferrets in Northcentral Montana

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Abstract.—The Phillips Resource Area of northcentral Montana is a prime candidate for reintroduction of black-footed ferrets from captive-breeding programs. Most of the land containing black-tailed prairie dog (*Cynomys ludovicianus*) colonies is administered by the Bureau of Land Management, U.S. Fish and Wildlife Service — Charles M. Russell Wildlife Refuge, and Fort Belknap Indian Reservation. Colony surveys in 1981, 1984, and 1988 reveal colony growth and indicate healthy prairie dog populations. In 1988, 255 colonies totaled 28,540 acres (11,550 ha) and contained 1,236,808 burrows. Using the method of Biggins et al. (1988), we delineated four complexes encompassing 68.5 percent of these colonies. The distances between complexes and the intervening colonies will give a measure of complex isolation but allow some degree of long-distance dispersal. To assess the potential of each complex, we apply the black-footed ferret Habitat Suitability Index models of Houston et al. (1986) and Biggins et al. (1988), and we introduce variable and model revisions. Revisions include modification of variable functions and addition of variables derived from the design of ecological reserves. Variables that assume direct estimates of prey density are separated from the main model but can easily be incorporated when future methodology and data become available. We also address the role of epidemiology, other nearby complexes and colonies, potential for prairie dog expansion, abundance of other predators, and future resource conflicts and ownership stability. We stress that HSI variable weights and relations and model form are flexible. Thus, we present the raw data and intermediate calculations.

Captive-reared black-footed ferrets (BFFs) are planned to be released into one or more prairie dog (*Cynomys* spp.) complexes in North America beginning in 1991 (USFWS 1988). Successfully established BFFs will be a major contribution to restored biodiversity of these unique communities. BFFs will likely be reintroduced into relatively large prairie dog complexes (clusters of prairie dog colonies) because of the spatial requirements of viable BFF populations. Because only two BFF populations have been studied, the goal of defining a complex operationally and understanding the functional role of its habitat attributes for BFFs has been impeded. In addition to this purely biological uncertainty, there are socio-political intricacies that must be accounted for (see Maguire 1986, Maguire et al. 1988). Nevertheless, states and provinces that contain potential complexes for BFF colonization require a screening process to rank the relative suitability of sites.

Any useful screening process should address at least the ecological variables required for successful BFF reproduction and survival. Fortunately, these life-history requisites are provided almost entirely by prairie dog populations (population descriptions in Clark 1986a). BFFs rely on prairie dogs for food and prairie dog burrows for cover and reproduction (Forrest et al. 1985, Houston et al. 1986). What we lack in specific knowledge of BFF ecology is partially compensated by theoretical simplifications stemming from its high trophic level, functionally and structurally simplified community, and behavioral specialization on a single prey type.

The original guidelines of Forrest et al. (1985) identified the critical habitat variables for BFF management and reintroduction. The Habitat Suitability Index (HSI) model produced by Houston et al. (1986) was based on Forrest et al. (1985) and attempted to specify the functions and values for critical biological variables pertaining to long-term maintenance of BFF populations. All five HSI variables were directly derived from prairie dog biology which afforded the HSI considerable breadth in its coverage of habitat components (see Farmer et al. 1982). Subsequently, Miller et al. (1988) and Biggins et al. (1988) slightly modified the original HSI and listed other considerations for appraising complex suitability: plague potential, canine distemper potential, future resource conflicts and ownership stability, and public and landowner attitudes. In part, these factors were originally discussed by earlier workers such as Cahalane (1954), Linder et al. (1972), and Erickson (1973), but it was not until after the Meteetsee studies that they were synthesized by Forrest et al. (1985) and Clark (1986b).

The main benefit of a suitability model is to join the variables together in meaningful groups and with relative weights. We refer those readers not familiar with basic quantitative concepts to the excellent review in USFWS (1981). These simple weights and relationships enable resource managers to screen potential sites more readily and to see the relative importance of variables. Managers can then set priorities for funding, manpower, and extent of sampling effort based on the variable importance. No doubt data will be adequate for some variables and incomplete for others. Consequently it is crucial that steps used to arrive at suitability results always be presented for each variable to allow partial and complete comparisons of whatever variables are measured by the manager.

HSIs and their variants are deliberately the simplest form of modelling. Yet two of the objections raised against their use on BFFs are that they are too "complex" and that

their calculation is time consuming. As for the complexity issue, anyone who fills out his own income tax forms should be at ease. As for time consumption, hundreds of man-hours are spent gathering the data for any of the current HSI models, and that is enough justification for one person to spend several hours with a calculator (all functions and relationships are available on any scientific calculator) for the very small number (±20) of potential translocation sites in North America. Moreover, in performing the calculations, decision-makers are likely to gain a better understanding and appreciation of the components of BFF habitat suitability.

The first detailed, state-wide assessment of potential BFF reintroduction sites was in the state of Montana (Clark et al. 1986a). After considering most of the suitability factors discussed above, Clark et al. (1986a) determined that the cluster of complexes in the Phillips Resource Area of northcentral Montana was ranked highest in the state. Our analyses and discussions are based on surveys of several hundred black-tailed prairie dog (*C. ludovicianus*) colonies in the Phillips Resource Area during 1981, 1984, and 1988. In 1988, cooperators gathered data on 255 colonies, totaling 28540 ac (11416 ha), which included the necessary information for evaluating current BFF habitat variables except for actual prairie dog densities.

This report summarizes our results and reevaluates the variables and variable functions currently being proposed or used in BFF habitat suitability analyses. For comparison, we apply the original HSI (Houston et al. 1986), the Rating Index of Biggins et al. (1988), and our revised HSI* (models and variables revised in this document will be denoted with an asterisk) to the Phillips Resource Area data as well as other measured complexes. We then discuss six other factors that bear upon suitability of the complexes in the Phillips Resource Area.

NORTHCENTRAL MONTANA — THE PHILLIPS RESOURCE AREA

The general ecology of the Phillips Resource Area has been described by several authors. Knowles (1982) evaluated prairie dogs on the Charles M. Russell National Wildlife Refuge (CMR). Clark et al. (1986a) reported on the 1981 and 1984 state-wide prairie dog surveys. Reading et al. (1989) described growth dynamics and biodiversity of selected colonies, mostly on lands managed by the Bureau of Land Management (BLM), but including privately-owned lands and lands under the ownership of the State of Montana.

Prairie dog colonies are found on lands under several categories of ownership: BLM, State of Montana, private, U.S. Fish and Wildlife Service-CMR, Fort Belknap Indian Reservation (FBIR), and Bureau of Reclamation (BR). The colonies on CMR and FBIR are still being reevaluated (and thus estimated in this document from prior surveys) with scheduled completion in the summer of 1989. The BLM and cooperators surveyed colonies in 1988 on BLM, state, private, and BR lands.

In this section, we integrate the results of the extensive 1988 colony survey of Phillips Resource Area and describe prairie dog features of the area that influence BFF suitability in relation to land ownership or status. In a later section we will analyze colonies as part of complexes using biological considerations.

Methods

The data used here were compiled and processed by J. Grensten and R. Reading; their methods are described in Reading et al. (1989). Burrow densities for each colony on BLM, BR, State, and private lands were measured in 1988. Burrow densities on CMR were taken as the average from Knowles (1982) and FBIR colonies were assigned the average burrow density for all known colonies in 1988. Although most surveys were conducted within the same season for all years, we did not adjust for the month-to-month variation in burrow counts which may be considerable (S. Forrest and L. Forrest pers. comm.). Furthermore, we have lumped colony surveys conducted between 1979 and 1982 into the year category of 1981 because most of the surveys did occur in 1981. Thus, statistical description of data involving 1981 surveys, and to a lesser degree all surveys, should be viewed as illustrating trend and is not intended for exact statistical inference. Statistical summaries and analyses were conducted on a Macintosh SE microcomputer using StatView 512+. Where necessary, variables were normalized by log transformation for analyses, but figures containing means and standard errors (SE) were calculated from untransformed data. Factorial analysis of variance (ANOVA), one-factor and two-factor repeated measures ANOVA, and the Fisher PLSD multiple comparison test follow Winer (1971). We used English units in most cases and list metric unit equivalents. The exception was in several of the figures, where only English units were used.

Results and Discussion

Figure 1 is a map of the area showing the colonies and colony complexes current through 1988. Numbers of colonies are classified by ownership (or land status) in Table 1. The proportion of colonies included in surveys covered more colony area over a greater diversity of land ownerships in 1988 than in 1981 and 1984 (Figure 2). In 1981 surveys were confined to BLM, State, and BR colonies. The survey of 1984 added a substantial proportion of colonies on private lands. As we became aware of the value of surrounding colonies and complexes to any potential reintroduction site, those colonies on neighboring FBIR and CMR were included in 1988. Thus, the year-to-year pattern is more indicative of the increasing scope of surveys through time, as well as the inclusion of other ownerships, than it is of actual differential colony formation and expansion relative to land status. Therefore, FBIR and CMR colonies are not part of the detailed colony survey instigated in 1981. This can be seen further in Figure 3 which shows how total colony size varies by land status year-to-year.

Figure 4 displays the values for burrow densities by land status in 1988. Note that these values are not the average burrow density but, instead, burrow densities were weighted by the corresponding colony size. This was accomplished by multiplying each colony size (within a land status category) by its density, summed within land status category, and then divided by total colony area within land status category. Ignoring burrow density for BR colonies (small sample size), burrow densities by land status appear uniform except for those on private lands. Not all prairie dog towns were sampled on private lands, which may have resulted in biased sampling of more productive colonies. BLM manages most of the prairie dog burrows (Figure 5).

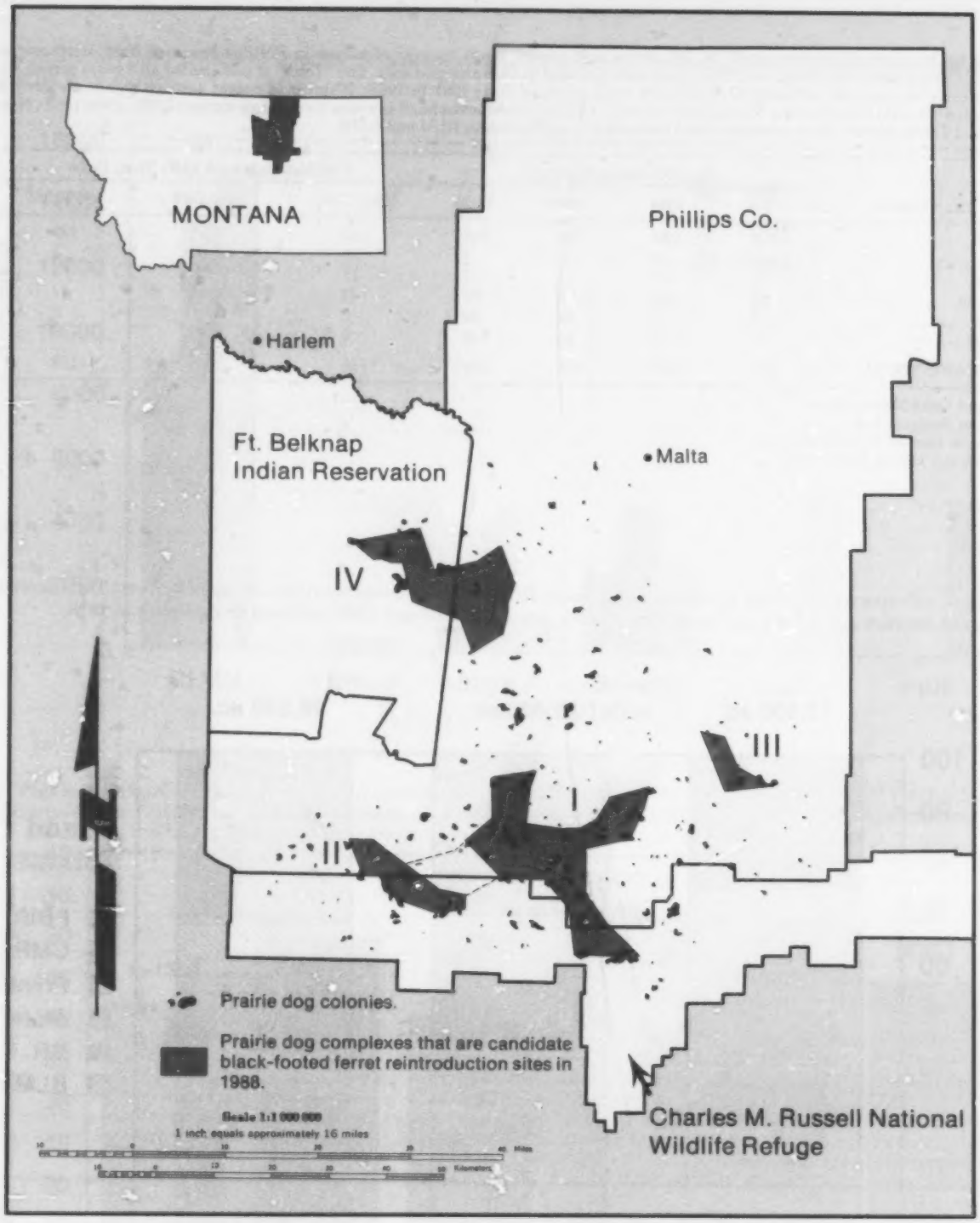


Figure 1.—Depiction of prairie dog complexes that are candidate reintroduction sites for the black-footed ferret in northcentral Montana, 1988. Prairie dog colonies are shown grouped into complexes which are delineated using the "7 km rule" of Biggins et al. (1988). Dashed lines connecting complexes I and II form a single alternative complex as described in text. This map shows colony-size modifications and additional colonies that are current as of August, 1989 but were not included in our present analyses (see Authors' Note). Consequently, some colonies appear as if they should have been included within a complex.

Table 1.—Numbers of colonies on BLM, BR, State, and private lands by year of survey in Phillips Resource Area, northcentral Montana. Colony data from CMR and FBIR lands were included in 1988 analysis only. The "Total" of colonies for all 3 years pertains to different colonies (e.g., 143 different BLM colonies were surveyed from 1981 to 1988). Number of repeat surveys on same colony is contained in the last three columns. For example, there is data on 109 different BLM colonies for all three surveys (1981, 1984, 1988). Note that Grand Totals include three colonies whose ownership is split between BLM and CMR.

Land Status	No. of Colonies Surveyed				Colonies Surveyed More Than Once		
	1981	1984	1988	Total	1981-1984	1984-1988	1981-1988
BLM[1]	114	129	136	143	113	122	109
BR[2]	0	4	5	5	0	4	0
State	15	13	11	17	11	9	7
Private	49	72	32	93	42	20	17
CMR[3]	0	0	59	59	0	0	0
FBIR[4]	0	0	15	15	0	0	0
GRAND TOTAL	178	218	258	332	166	155	133

[1]Bureau of Land Management
[2]Bureau of Reclamation
[3]Charles M. Russell Wildlife Refuge
[4]Fort Belknap Indian Reservation

Figure 2.—Proportion of colony acreages falling under different land ownerships for each year of survey. Total acreage of surveyed colonies appear at top of each year column. Data for FBIR and CMR are from studies prior to 1988.

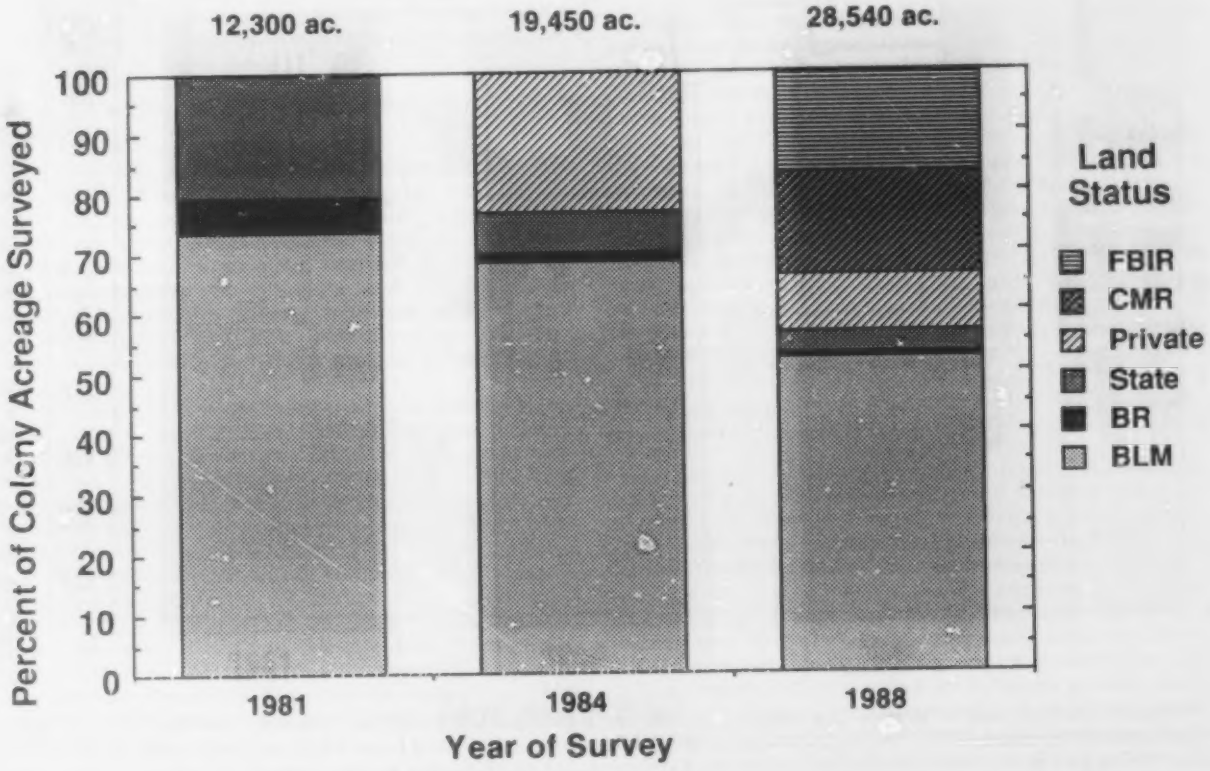


Figure 3.—Total acreage of colonies by land ownership for each year of survey. Data for FBIR and CMR are from studies prior to 1988.

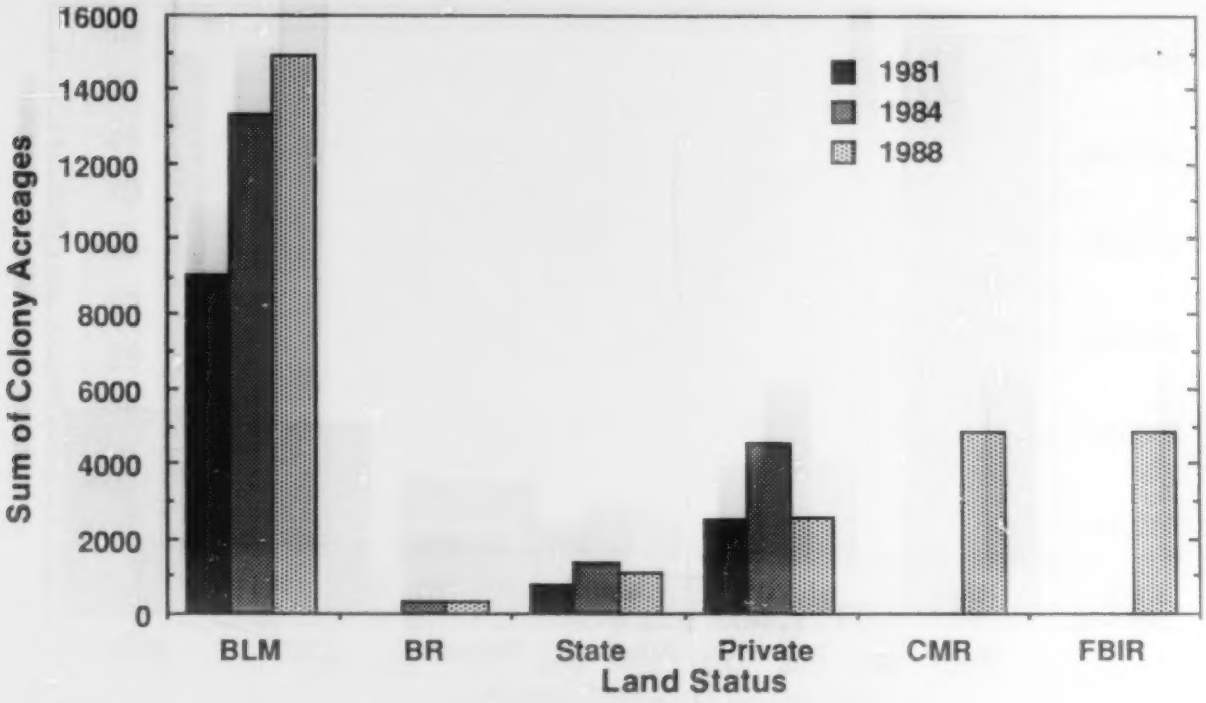


Figure 4.—Burrow density by land ownership in Phillips Resource Area from 1988 survey. CMT density is from Knowles (1982). FBIR is estimated as the mean of surrounding colonies in Phillips Resource Area from 1988 survey.

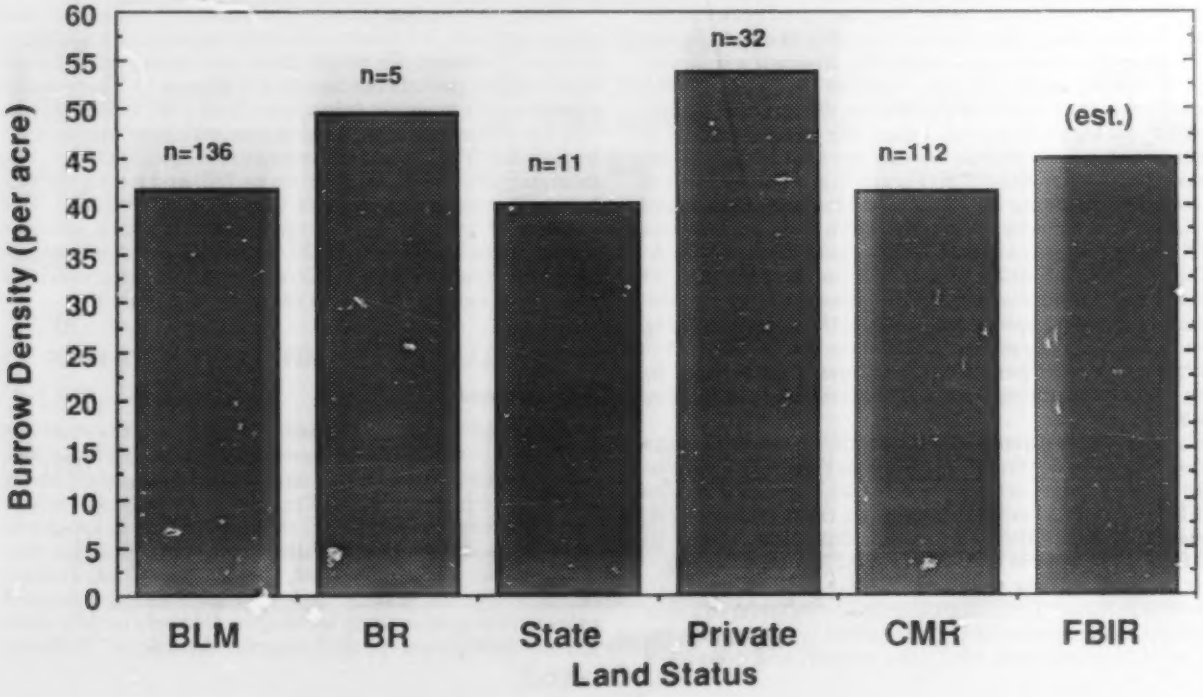
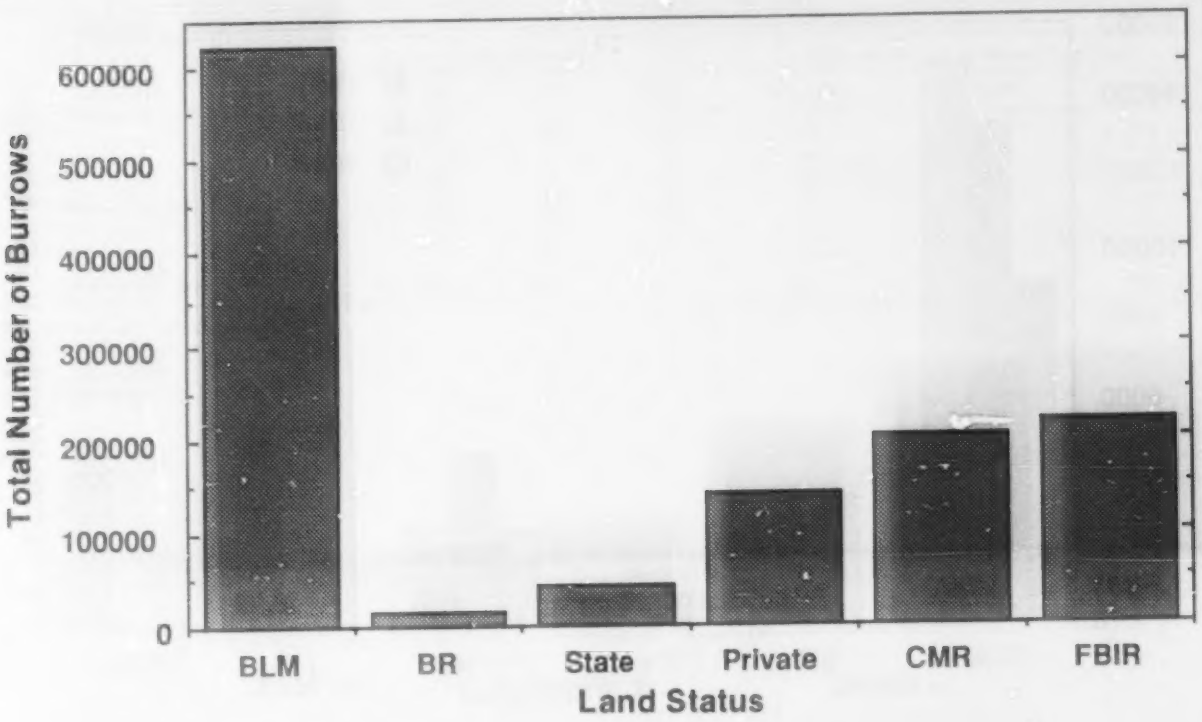


Figure 5.—Total number of burrows from all surveyed colonies in 1988, by land ownership. Data for FBIR and CMR are estimated from studies prior to 1988.



The size of colonies and the distribution of colony sizes is an important component of BFF site suitability (Forrest et al. 1985, Houston et al. 1986). Because most colonies are small, the resulting distribution is highly skewed (Figure 6). There is little value in comparing frequency distributions of colony sizes directly without reference to the assumptions that incorporate reserve design and prairie dog-BFF biology. However, when the size category is categorized by land status, we can see that mean colony size is far greater on the FBIR (Figure 7). Excluding the five BR colonies and using log-transformed colony sizes, there are significant differences in paired comparisons between FBIR with BLM, private, and CMR colony sizes (ANOVA: n=253, overall P=0.0125, Fisher PLSDs significant at 99 percent). In general, surveys will be biased against smaller colonies in most sampling regimes and this bias is likely to be more severe in the present FBIR data set. In this case it is difficult to separate true management differences in these colony attributes from differences due to sampling bias and error.

There is also an increase in mean colony size within the land-status category from 1981 to 1988 (Figure 7). For combined BLM, private, and State colonies, there is a highly significant trend of colony expansion from 1981 to 1984, decreasing to a positive but nonsignificant rate of expansion from 1984 to 1988 (one-factor ANOVA repeated measures: n=133, treatment P<0.0005, Fisher PLSDs significant at 99 percent). The design is unbalanced (refer to Table 1) and the same conclusion was obtained for separate pairwise ANOVA analyses, 1981-1984 (n=166) and 1984-1988 (n=155), indicating no obvious bias in which colonies were more subject to one, two, or three surveys.

Next, we consider interaction between land status and colony growth. We examined colony expansion within the subset of colonies for which there are colony sizes for all three survey periods (as depicted in Figure 8). There was a significant increase in colony size from 1981 to 1988 but no reliable difference in expansion rate with land status (two-factor ANOVA repeated measures: n=133(109,7,17), treatment P<0.0005, land status p=.785) and no interaction between expansion rate and land status (P=0.943). The pattern of growth may correspond with management shifts: around 1984 the BLM began its shooting control program. Reading et al. (1989) contains a full discussion of expansion rates for a subset of the data used here.

HSI VARIABLES AND MODEL EVALUATION

Background

Habitat Evaluation Procedures (HEP) and the resulting HSI model standards were developed by the USFWS (1980, 1981) and have been widely used in environmental impact studies and in evaluation of species-habitat relationships (Cole and Smith 1983, O'Neil et al. 1988, see also articles in Bovee and Zuboy 1988). Williams (1988) concludes that HEP represents "a structured, systematic process and use of mathematical models makes HEP a decision-support process that is superior to techniques that rely largely upon professional judgment and superficial surveys." Williams

Figure 6.—Frequency distribution of all 255 colonies included in analysis of Phillips Resource Area for 1988. The first size category contains all colonies of size 0<50 acres (0<20 hectares) the second size category of 50<100 acres (20<40 hectares), etc. Data for FBIR and CMR are estimated from studies prior to 1988.

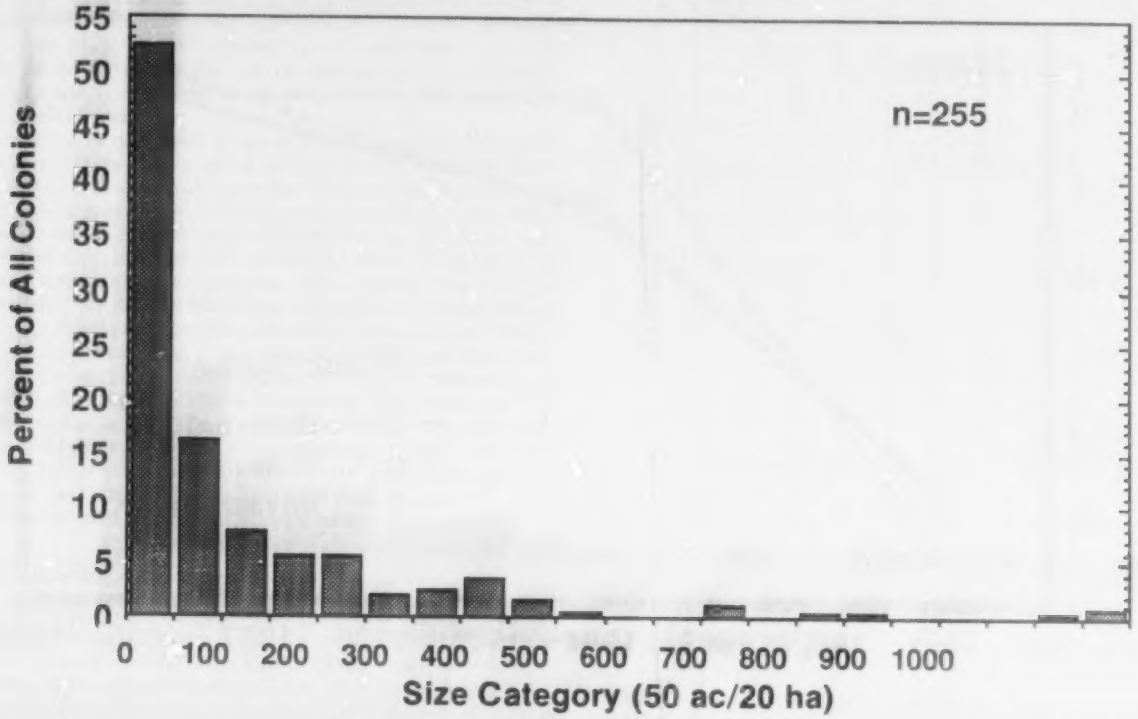


Figure 7.—Mean colony size (acres) by year and land jurisdiction. For ease of interpretation, we present the arithmetic mean (+1 standard error) instead of the geometric or log-transformed mean which is used in analyses. Data for FBIR and CMR are estimated from studies prior to 1988.

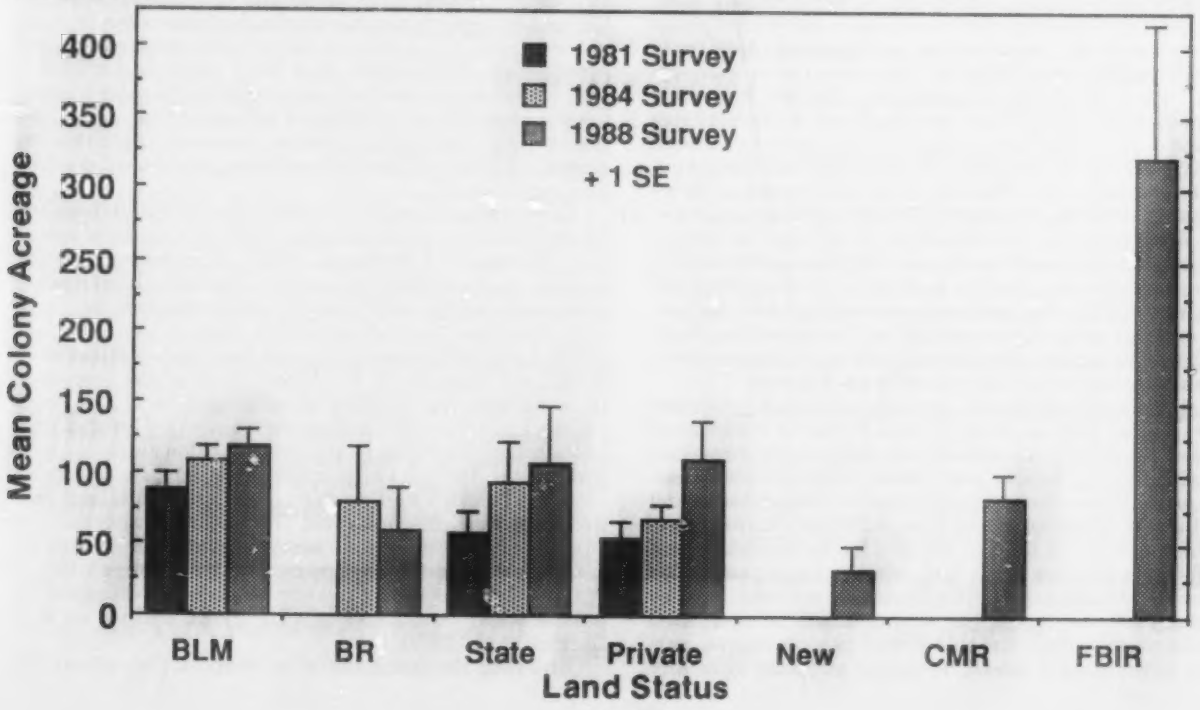
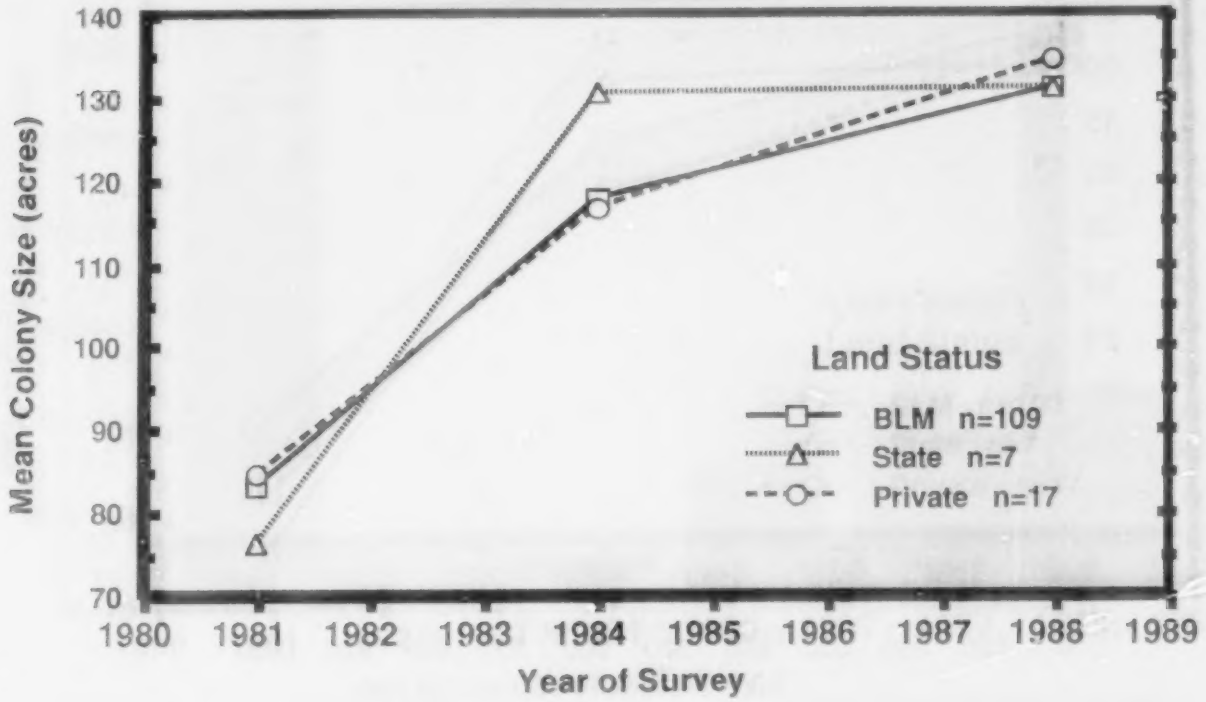


Figure 8.—Depiction of colony growth by year of survey (1981, 1984, 1988) and by land ownership. Ownerships containing sufficient data were included in analysis. Arithmetic mean colony sizes are presented but log-transformed data was used in ANOVA analyses.



(1988) quotes Urich and Graham's (1983:221) assessment that "[HEP is] a logical wildlife management area planning procedure through which an interdisciplinary team can inventory existing conditions, draw inferences about habitat suitability, and simulate management practices to display positive and negative consequences of management." Because the HSI standard is a flexible and easily comprehended model form, we employed it originally in Houston et al. (1986) and continue to use its basic tenants as do (implicitly or explicitly) all other BFF biological suitability models to date. Houston et al. (1986) realized, as we do now, that the major handicap in constructing a model of BFF species-habitat relationships is the lack of proper model validation (see Marcot et al. 1983), except for expert opinion or "species authority validation" (Zuboy 1981, Cole and Smith 1983). This predicament is dictated by the species' extreme rarity. There are just too few population data, and both life history assumptions and mathematical relationships between habitat variables are tenuous.

Yet it is inescapable that management must determine where BFFs will be reintroduced and whatever the decision process, it will be based on the same amount of information but with varying amounts of theory, comparative knowledge, and arbitrariness. The purpose of a simplified model is to balance these considerations judiciously thereby forcing us to arrive at a small set of discrete variables and weigh their relative merit and relative importance. The choice of variables and their functions will no doubt be arbitrary to some degree, but we hope it will be minimized by this partitioning. An HSI model can be viewed as a static, deterministic model. It cannot simulate or in any way model the probability of population stability or persistence because it is neither dynamic nor stochastic. An HSI merely assesses the suitability of a habitat based on life-history requirements so that comparisons can be made among areas. It is a relative index at the population level. Most people will assume that more suitable habitats of more suitable sizes and arrangements will be more likely to sustain populations over longer periods of time. Other variables (land ownership, plague potential, nearby complexes, etc.) can qualitatively address questions of stability and persistence.

One strategy used by Houston et al. (1986) in building an HSI was to incorporate principles of ecological theory (e.g., Flather and Hoekstra 1985), comparative mustelid ecology, and quantitative ecology. Through the process of continuous model validation by expert opinion, the variables, functions, and relationships used in Houston et al. (1986) have been reevaluated and modified by Miller et al. (1988) and Biggins et al. (1988). Most of the suggested changes were the addition of epidemiological and sociopolitical factors, with changes to the original habitat variables being minor, as in the case of value shifts, or arbitrary, as in the case of variable deletions. Furthermore, ecological theory and mathematical and statistical relationships were misconstrued. The major advancement by Biggins et al. (1988) was a semi-standardized method for defining the complex perimeter allowing computation of "proportion of complex containing colonies (occupied by prairie dogs)" and its suitability index, defined as P in Biggins et al. (1988).

Knowing the perimeter of a complex also allows the

comparison among complexes of important characteristics of BFF habitat that are used in reserve design, landscape ecology, and biogeography, particularly those of shape and linearity. Two other such variables, patch or island (colony) size distribution and a readily measurable aspect of their spatial distribution, were already included in Houston et al. (1986) as V1 (colony size distribution) and V4 (nearest neighbor or intercolony distance). Figure 10 summarizes the original Houston et al. (1986) HSI variables and model form.

Biggins et al. (1988) chose a single variable P to summarize all the varied spatial attributee of a complex. They converted P to a suitability index (Figure 7 in Biggins et al. 1988). Along with colony area and burrow density, they formulated a three-variable Rating Index (R); thus, two-thirds of this method for complex's rating involves total colony area and total complex area (Figure 10). We have calculated Rs for our Montana data and, for comparison, from the Meeteetse complex (1984 data), Cumberland Flats — Wyoming (Area II) of Houston et al. (1986), and the hypothetical example used in Biggins et al. (1988), referred to as the RSG Example. We have also revised the Houston et al. (1986) variable functions, added variables now derivable from the perimeter, and suggest some variable relationships. Three classes of attributes are presented and discussed: pure spatial attributes, biological spatial attributes, and food, reproduction and cover attributes.

Pure Spatial Attributes

The compelling and extensive literature in spatial ecology regarding population dynamics, predator-prey dynamics, reserve design, and epidemiology convinced us to include three variables describing pure spatial properties of a complex. Our own work clearly points to how critical spatial heterogeneity (patch dynamics) will be in BFF-prairie dog population stability (Klebanoff et al. in ms.). We use "pure" spatial properties in the sense of quantitative description that is independent of BFF biology. We also refer to these spatial properties as reserve design components because a complex, the unit of habitability for BFFs, is likely to serve as a sustainable population reserve.

The first variable is V1 (Houston et al. 1986) except, per recommendation of Biggins et al. (1988), only colonies 5 ha or greater are considered. This change is denoted by referring to its revised form as V1*. [An unrelated benefit of this rule is that it eliminates sampling bias against very small colonies, although smaller colonies may be critical in assessing expected growth of complexes (Reading et al. 1989)]. V1* describes the distribution of colony sizes (see rationale and formulation in Houston et al. 1986). Values of V1* are higher for complexes that contain larger colonies as opposed to many small colonies. V1* implies that bigger colonies are better (Houston et al. 1986, Biggins et al. 1988).

The second variable can be described as Complex Shape (CS) and a form of it has been used elsewhere in the ecological literature (Patton 1975, Bowen and Burgess 1981, Forman and Godron 1986). It measures the "roundness" of a complex by comparing its area-to-perimeter ratio to that of circle with identical area. We take the inverse in order to normalize the values between 0 and 1:

$$CS = \left(\frac{\text{Complex Perimeter}}{2\sqrt{\text{Complex Area} \bullet \pi}} \right)^{-1}$$

Figure 9A.— V4* — Nearest-neighbor or Intercolony Distance. $V4^* = 1 - (1 + 25e^{(-X)})^{-1}$

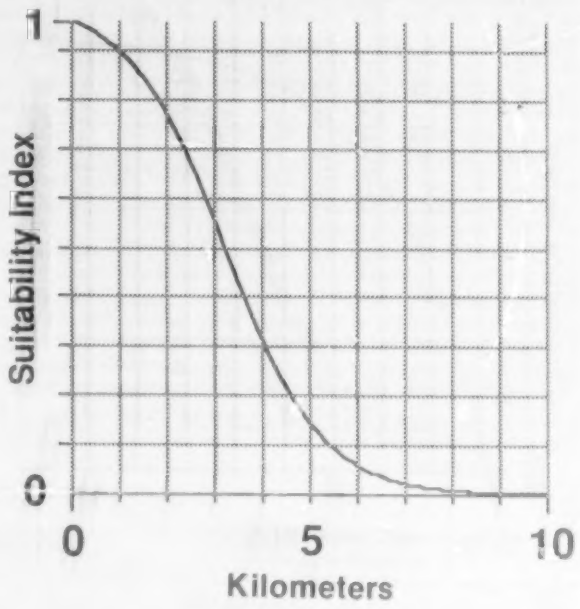


Figure 9B.— V3 — Burrow Density. $V3 = (1 + 15e^{(-.06X)})^{-1}$

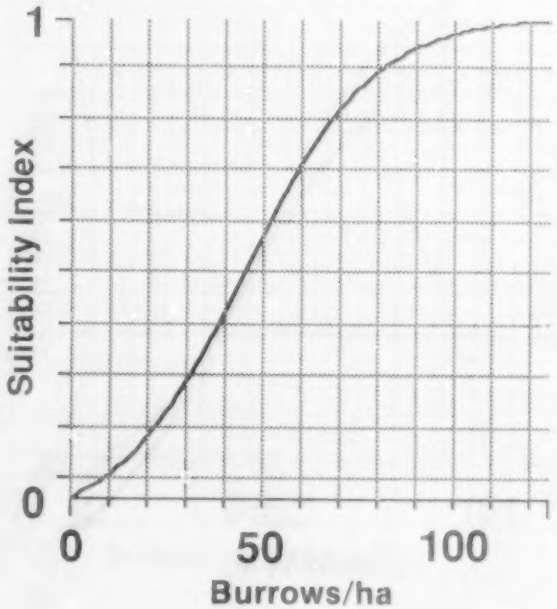


Figure 9C.— V2* — Total Colony Area Within Complex. $V2^* = 1 - 1.1e^{(-.00025X)}$

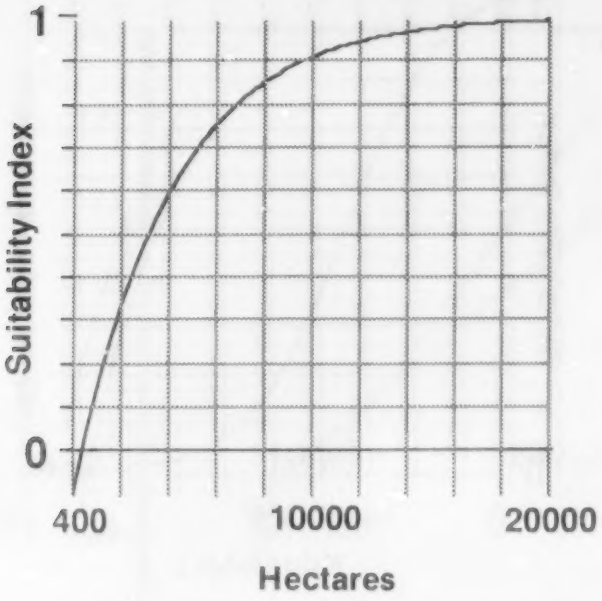
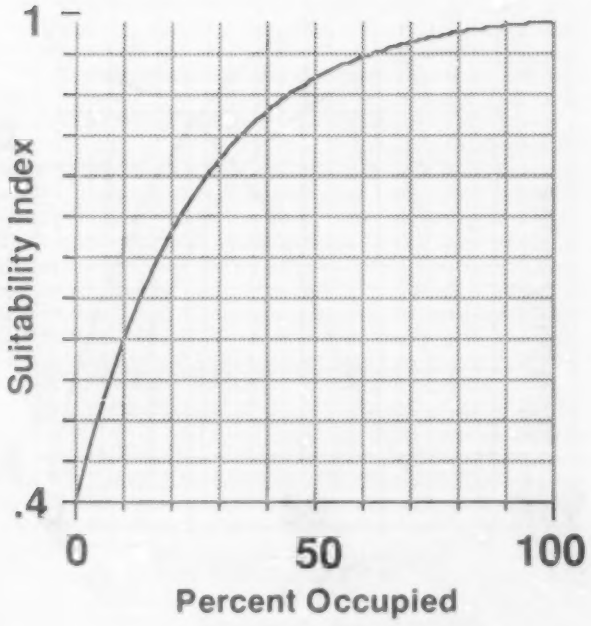


Figure 9D.— P* — Percent of Complex Occupied by Colonies. $P^* = .4 + .6\,(1 - e^{(-.04X)})$



CS implies that those complexes with more edge exposed to "hostile" territory (e.g., star-shaped or having numerous peninsulas) are less desirable than rounder ones.

The third variable is the ratio of the complex's minor axis to its major axis. The axis ratio (AR) gives small values for linear (elongate) complexes and a value of one for "compact" complexes. The major axis is the longest dimension of the complex. The minor axis is the longest dimension of the complex that is perpendicular to the major axis. AR is also in accordance with Biggins et al. (1988): the more linear in shape the complex, the less desirable.

All three variables are simple to calculate, range from 0-1, and are highly intuitive. But more importantly, these variables work in concert and are obviously related to each other to some extent and yet remain independent measures to some extent. There is always potential compensation among variables that are related (co-linear) to some degree as in any habitat and/or suitability model. Therefore, compensation is not only an essential process but is part of the rationale in combining variables in a model. Likewise, any variable or parameter in a statistical or mathematical relationship (e.g., the mean and variance of a distribution) can be taken in isolation and shown to be woefully inadequate by itself, especially when extreme examples are used.

Biological Spatial Attributes

In this category we consider two spatial variables whose functions and values are directly dependent upon BFF biology. Both P, the suitability factor for percent complex (Figure 7 in Biggins et al. 1988), and intercolony distance (within a complex) in the form of mean nearest neighbor (V4 of Houston et al. 1986) assess a different aspect of colony distribution within a complex. P calculates the ratio of total area while V4 addresses the mean contagion or clumping (of discrete colony areas) and forces a within-complex scale of distance by using the critical threshold of 4.4 mi (7 km), just as the 4.4 mi (7 km) rule was applied to defining the complex perimeter, shape, and area. Because the original V4 used 7.5 mi (12 km, dispersal distance) as the threshold distance and we have modified it here to reflect a maximum distance of more common movement (4.4 mi, 7 km), we will refer to it by the notation V4* (Figure 9A).

Despite the artificial and extreme cases of colony distributions used by Biggins et al. (1988), for realistic distributions there is little doubt that colonies averaging, say, 3.8 mi (6 km) in intercolony distance (nearest neighbor) are less suitable habitat than a complex with colonies averaging 0.6 mi (1 km) apart. Fortunately, most actual intercolony distances in complexes do not range much above 0.6-1.2 mi (1-2 km, but see distribution within Mellette County, South Dakota, complex [e.g., Clark et al. 1986a Figure 9g]), and consequently suitability values remain high for most sites we have seen. Thus V4 operates more as a filter for complexes that have otherwise good qualities but that unfortunately have highly dispersed colonies. In short, we agree with general patch theory (as applied to within-complex dynamics) and in particular with Biggins et al. (1988:11): "we choose to base our revised model on the premise that 'the bigger *and* the closer the colonies the better.'" (their emphasis); the same conclusion reached earlier by Houston et al. (1986). We consider the implications of colony proximity and clustering on epidemiological factors to be an eminent but separable issue from the present HSI formulation.

We suggest using a different function for the suitability index, P, of Biggins et al. (1988:Figure 7). There is no equation for the function but the drawn figure portrays a sigmoidal curve (e.g., the type of curve in Figure 9B) starting at 0 percent (colony area to complex area) giving a Suitability Index value of 0.4. Suitability gradually increases with percent, rapidly increasing with mid-range percentages, and finally gradually flattening again at higher percentages. We have modified this curve (P*, Figure 9D) in order to increase suitability values rapidly immediately above 0 percent and only diminish this rate of increase as intermediate and high percentages are reached. A slow increase at the lowest values of percent seems contrary to our expectation that small differences in colony area percentage of a complex are most critical at the lowest values. Hence, the difference between 0+ percent and 5 percent will result in a far greater increase in suitability then will the difference between 50 percent and 55 percent. The starting point for the Suitability Index, 0.4, was that Mellete County supported a BFF population despite its 1 percent value (Biggins et al. 1988). Our revised P* was based on the range of values for known complexes.

Food, Reproduction and Cover

Until an economical and reliable method is developed for estimating prairie dog densities, we must rely on the strong assumption that an increase in total colony area, V2, and burrow density, V3, of Houston et al. (1986) will be highly correlated with an increase in food, reproductive, and cover value.

Preliminary results indicate a usable relationship between active/inactive burrows and prairie dog density for a wide range of densities (0-6.0+ per ac, 0-15+ per ha) for white-tailed prairie dogs (*C. leucurus*) (D. Biggins pers. comm.). The regression must be recalibrated with population data from black-tailed prairie dogs and this should be completed during summer, 1989. Until this relationship is developed and implemented, measurement of BFF suitability involving black-tailed prairie dogs will continue to rely on the inexact but strong correlation between burrow density and prairie dog density (Forrest et al. 1985). If the relationship is accepted, then complexes such as those in Phillips Resource Area will be resurveyed or resampled to distinguish active from inactive burrows. At that time HSI models can embody fully those variables directly related to prey densities and be substituted for the V3 of our present formulations. For example, D. Biggins and B. Miller (Interstate Coordinating Committee 1989) proposed this preliminary modification of R: R = Total Prey × Index Factor for Maternal Value of Habitat × P. In our present model maternal value of habitat is contained in the assumptions and suitability functions (rationale in Houston et al. 1986).

Variable Functions

We will not belabor the need for nonlinear relationships in suitability factors (e.g., Houston et al. 1986) versus linear ones (e.g., A [area] and D [burrow density] in RI of Biggins et al. 1988). The importance and realism of nonlinear processes (diminishing returns, interest rates, sigmoidal responses, etc.) in nature is overwhelming and irrefutable. We have outlined the reasoning for the form of variable functions in Houston et al. (1986) and in our earlier discussion. In conclusion, for those variables transformed to a suitability factor we present our best choice for those functions (Figs. 9A-D) based on existing data and expert opinion.

We have discussed V4 of Houston et al. (1986) and its modification to V4*. V3, the function for burrow density remains unchanged (Figure 9B). V2, the suitability of total colony area has been modified (V2* in Figure 9C) to accommodate the larger complexes that have been surveyed in the last 3 years (D. Biggins pers. comm.). V2* now assigns complexes totaling less than 1000 ac (400 ha) of colony area a suitability of 0 (Biggins et al. 1988). Suitability rapidly increases with total colony area until above 25000 ac (10000 ha) and then has a "diminishing return." In other words, adding 2500 ac to a 7500 ac (1000 ha to a 3000 ha) complex increases its suitability index disproportionately more so than would adding 2500 ac to a 47500 ac (1000 ha to a 19000 ha) complex.

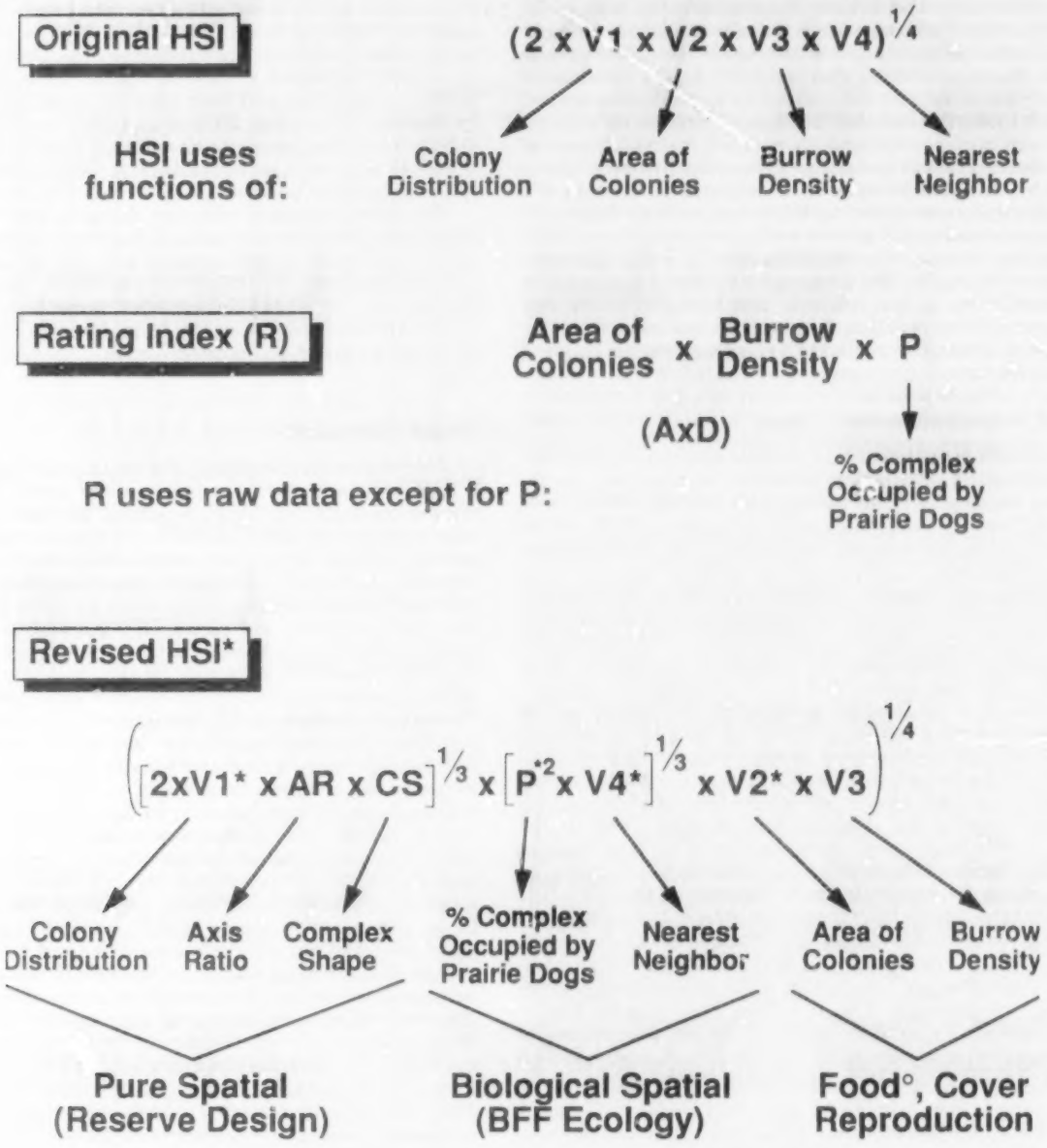
We encourage users who may disagree with the exact shape and range of our variable functions to make their own modifications and recalculate the corresponding values. For example, D. Biggins (pers. comm.) believes that the range for V2* should be extended upwards to 40000+ ha to include some exceptionally large Mexican complexes. This can be easily accomplished with a calculator in minutes.

Model Formulation

We contend that the most important part of generating a BFF HSI is to select the most salient variables and to choose carefully the functions which describe suitability and relationships based on data and expert opinion. Compared to other species for which HSIs have been constructed, the case of modeling habitat suitability for BFFs essentially precludes standard validation routes because of the paucity of data addressing BFF population and community patterns and because of their present extirpation in the wild. Some biologists may contend that the Meeteetse BFF study has established a solid knowledge of BFFs. The three-year Meeteetse study documented the possible disequilibria of a single population, but there is an enormous difference between a single well-studied population and the pattern that emerges from many studies of populations within a species, particularly carnivore species. The use of data to validate HSI models requires multiple (population) sources to avoid unique, historical, or other initial conditions that may not be representative or typical. Clearly, it is misleading and unproductive at present to exert ourselves in an attempt to be overly specific about formulating an exact model of variable relations when our best bet is to choose the variables, arrive at the variable functions as accurately as we can (because that is where the existing data and expert opinion is most applicable) and then find the simplest way of combining the variables after weighting them. We list these variables and HSI formulations in Figure 10. We have deliberately excluded V5 (Houston et al. 1986), the actual prairie dog density of a complex, because most surveyors have regarded it as logistically impractical (but see discussion above under Food, Reproduction and Cover).

We have given our reasoning for Pure Spatial and Biological Spatial variable groups and their compensatory nature. The grouping is depicted in the revised HSI* (bottom of Figure 10). V2* and V3 are agreed by all experts to be of singular importance and are thus kept separate. The difficult question is "How do we weight the relative importance of these variables and variable groups?" Biggins et al. (1988) gave equal weight to their spatial variable, P, and to Area of Colonies and to Burrow Density. Thus, one-third of their HSI "weight" is carried by spatial considerations.

Figure 10.—Schematic of three HSI models referred to in text.



°Note: Actual prairie dog density (V5) is a separate variable (see text).

In contrast, we have given one-half the new HSI*'s weight to all spatial variables combined, with one-quarter of the weight going each to V2* and V3, the suitabilities from Area of Colonies and Burrow Density. These weights are based on overall opinion and are no more or less realistic than the exactly equal weights in the original HSI and R.

In keeping with the variable weights expressed in R, we have also computed an alternative HSI*, Alt.HSI*. The formulation combines all five spatial variables and we give that grouping the same weight (one-third) as V2* and V3. In this way, compared to HSI*, spatial considerations are deemphasized relative to the increased weight of burrow density and colony area. We cannot overstress the idea that these model forms are not written in stone but are very easily modified by any person or committee who wishes to reweight the variables or variable groups. HSI "models should be viewed as hypotheses of species-habitat relationships rather than statements of proven cause and effect relationships" (Schamberger et al. 1982). For these reasons we list below all pertinent data for candidate complexes.

SUITABILITY OF THE PHILLIPS RESOURCE AREA REINTRODUCTION

We delineated four complexes as shown in Figure 1. Note that the Southcentral complex (I) and the CMR complex (II) are combined to form a fifth complex which we refer to as CMR+SC in Tables 2-4. We present a summary of the raw data in Table 2. Suitability Index values and calculations of R, HSI, HSI*, and Alt.HSI* are in Table 3. We review other factors in this section that bear upon their suitability. We follow the order of factors as listed in Biggins et al. (1988:Figure 8). The description and interpretation of these factors is ours except in reference to the categorical description of "developmental potential" and "land ownership patterns" found in Miller et al. (1988).

Epidemiology

The plague and canine distemper potential of an area is critical. We began interviews with regional veterinarians, selected ranchers, and land managers in 1985. These indicate that plague has not been recorded in the region in recent years. However, canine distemper is evident in domestic and wild carnivores. In 1989, we will begin more systematic surveys of these two diseases. The Cully (1989) contribution to this volume serves as an overview and as background for considering and managing plague in prairie dog colonies.

Other nearby complexes and colonies

This factor should include number, size, and direction of surrounding colonies (i.e., how many sides of the complex are near other colonies or complexes) and distance of colonies/complexes from periphery of candidate complex. Figure 1 reveals the proximity of the complexes, including a large number of large colonies that form "stepping stones" between Southcentral (I), Southeastern (III), and FBIR (IV). The influence of these and other colonies that are not included in any of the complex configurations can be summarized as follows: All complexes (I+II+III+IV) total 19528 ac (7903 ha) or 68.5 percent of all colonies included in the present 1988 analysis of Phillips Resource Area (Grand Total). The remainder of 31.5 percent of the Grand Total, or nearly a third of the colony area, is between the complexes and immediately surrounding them. These are conservative estimates of total colony area because not all existing colonies were surveyed in 1988. We can account for 9.5 percent (2697 ac, 1093 ha) of the Grand Total within 4.4 mi (7 km) of complex perimeters (see Table 4 for breakdown by complex). This leaves most of the remaining 22 percent (6289 ac or 2545 ha) of the Grand Total colonies as "stepping stones" among the complexes. Holding all other factors constant, the relative isolation of the Meeteetse (see Clark et al. 1986b) and Cumberland Flats (T. Clark Unpub. Data) complexes, substantially lowers their suitability compared to the Phillips Resource Area complexes.

Table 2.—Summary data for Phillips Resource Area complexes. The complex labeled CMR+SC (I+II) is the combined complex formed by connecting CMR (II) and Southcentral (I). Data are used to calculate variable and habitat suitability values contained in Table 3. Included for comparison are same data for Meeteetse and Cumberland Flats (Area I and Area II of Houston et al. 1986) and the RSG Example of Biggins et al. (1988).

Complex Name	Complex Area acres (ha)	Complex Per.[1] miles (km)	No.[2] Cols.	ΣColony Area acres (ha)	Percent[3] Colonies	Burrows per acre (ha)	N-N[4] miles (km)	Total Burrows (AxD)[5]
Southcentral (I)	93376 (37788)	80 (128.7)	58	9862 (3991)	10.56	39.9 (98.7)	.519 (.835)	393736
CMR (II)	17088 (6915)	25.5 (41.0)	17	2662 (1077)	15.58	36.8 (91.0)	.442 (.712)	98056
Southeastern (III)	10688 (4325)	21.2 (34.1)	11	1269 (514)	11.87	40.6 (100.4)	.482 (.775)	51537
FBIR (IV)	51840 (20979)	52 (83.7)	23	5685 (2301)	10.97	46.0 (113.6)	.754 (1.214)	261406
CMR+SC (I+II)	130176 (52681)	105 (168.9)	79	12629 (5111)	9.70	39.2 (96.8)	.548 (.882)	494920
Meeteetse (1984)	33280 (13468)	35.5 (57.2)	30	7124 (2883)	21.41	23.1 (57.0)	.572 (.920)	170430
Cumberland Flats	37274 (15085)	44 (70.8)	28	13577 (5494)	36.42	15.1 (37.3)	.621 (1.000)	205001
RSG Example	19069 (7717)	34.2 (55.0)	19	9172 (3712)	48.10	12.1 (30.0)	.498 (.802)	111360

[1]Perimeter of the complex delineated using Biggins et al. (1988) method.
[2]Total number of colonies in the complex.
[3]Ratio of ΣColony Area/Complex Area.
[4]Mean singular nearest neighbor distance for the colonies in the complex.
[5](AxD) refers to raw data grouping used by Biggins et al. (1988): ΣColony Area x Burrows per ha.

Table 3.—Variable and habitat suitability values for Phillips Resource Area complex candidates. Included for comparison are same values for Meeteetse and Cumberland Flats (Area I and Area II of Houston et al. 1986) and the RSG Example of Biggins et al. (1988). Variable values are calculated from suitability index functions described in text. Spatial variable groupings are intermediate steps. Alt. Spatial refers to alternative grouping of all five spatial variables of HSI* (see text); this grouping is then used to compute Alt. HSI*. P is suitability index function of percent colonies, V1* of colony distribution, AR of axis ration, CS of complex shape, V4* of nearest neighbor, V2* of Σcolony area within complex, and V3 of burrow density.

Complex Name	P	V1*	AR	CS	P*	V4*	V2*	V3	Pure Spatial	Biol. Spatial	Alt. Spatial	HSI (Orig.)	R	HSI*	Alt. HSI*
Southcentral (I)	.495	.033	.785	.535	.607	.916	.594	.961	.302	.696	.459	.446	194899	.589	.640
CMR (II)	.570	.212	.330	.718	.678	.925	.160	.940	.465	.752	.591	.460	55892	.479	.446
Southeastern (III)	.515	.149	.507	.683	.627	.920	.033	.965	.469	.712	.578	.378	26542	.320	.263
FBIR (IV)	.500	.110	.690	.613	.613	.881	.381	.984	.378	.692	.512	.495	130703	.560	.577
CMR+SC (I+II)	.480	.029	.690	.481	.593	.912	.693	.957	.269	.684	.429	.462	237562	.591	.658
Meeteetse (1984)	.680	.219	.393	.719	.745	.909	.479	.671	.499	.796	.630	.590	115892	.598	.587
Cumberland Flats	.845	.215	.287	.615	.860	.902	.722	.385	.423	.874	.608	.613	205001	.566	.553
RSG Example	.930	.221	.667	.566	.912	.918	.565	.287	.551	.914	.710	.520	103565	.535	.487

Table 4.—Characteristics of colonies surrounding candidate complexes. All colonies within 7 km of complex perimeter are included. Percent Cols. is the percent of all colonies in the 1988 data set for Phillips Resource Area.

Complex Name	No. Cols.	Σ Colony Area acres (ha)	Total Burrows	N-N miles (km)	Percent Cols.
Southcentral (I)	40	1884 (762)	66342	.984 (1.583)	6.600
CMR (II)	16	796 (322)	25978	1.286 (2.070)	2.789
Southeastern (III)	3	68 (28)	2963	1.800 (2.893)	.238
FBIR (IV)	8	333 (135)	17158	.890 (1.432)	1.167
CMR+SC (I+II)	51	2296 (930)	81718	1.053 (1.694)	8.044

Potential for prairie dog expansion

We have documented significant colony growth in Phillips Resource Area. Indications are that management by BLM, the majority land holder, can influence the rate of colony growth (J. Grensten pers. comm.). Reading et al. (1989) corroborated these findings and further revealed that most of the expansion rate is contributed by smaller colonies, although most of the absolute area expanded is contributed by larger colonies. The large proportion of colonies less than 50 ac (20 ha; see Figure 6) is greater than most areas for which there is comparable data and therefore may imply a greater potential for expansion. This factor should be explored in detail for judging suitability of translocation sites.

Abundance of other predators

The review of Phillips Resource Area by Reading et al. (1989) in this volume regarding diversity and abundance of some terrestrial and avian species associated with prairie dogs does not point to any conditions that could be deemed "very high predator densities" (see Forrest et al. 1985). More systematic surveys of associated vertebrate species, especially predators, will begin summer, 1989.

Future resource conflicts and ownership stability

We devoted a prior section to describing the relationship between colony attributes and land ownership within Phillips Resource Area as a whole. BLM and CMR control the vast majority of colony area in the complexes (Figure 11) with the obvious exception of FBIR (IV). In terms of the variable "land ownership patterns" of Miller et al. (1988:Variable 6), the Phillips Resource Area complexes receive the highest rating (6 out of 6) because land is most or all federally owned.

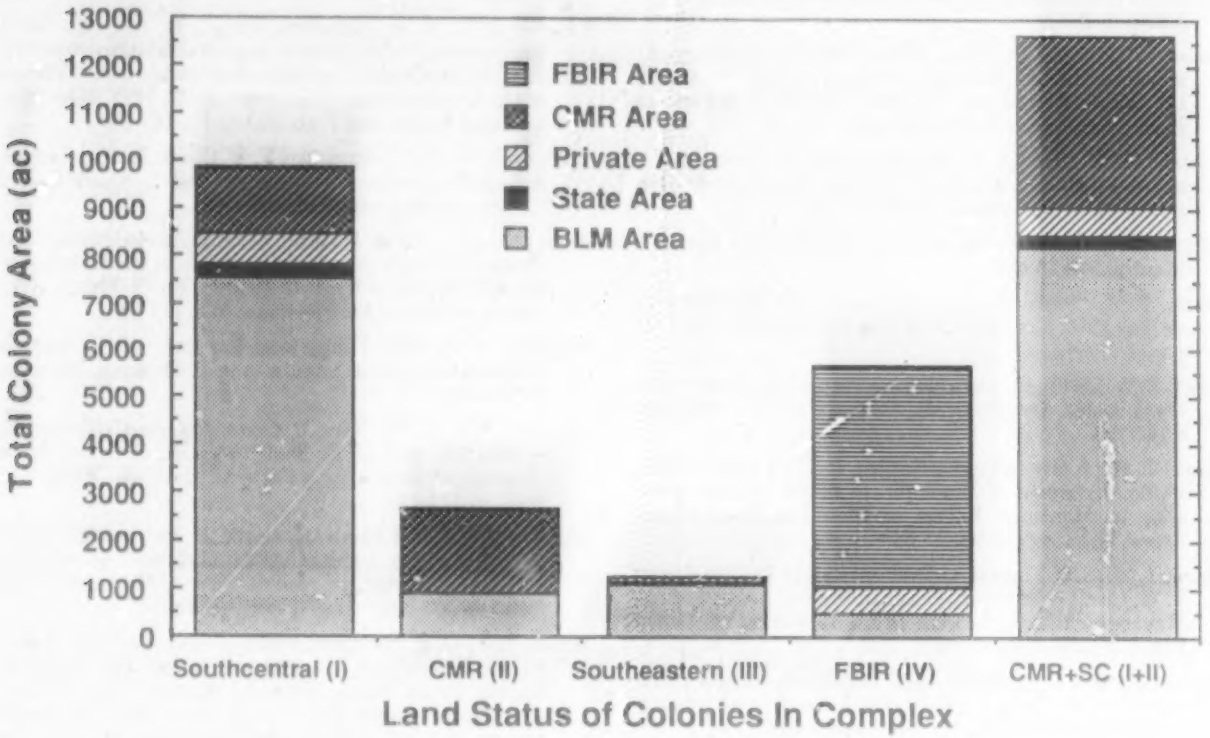
Public and landowner attitudes and their potential to change

Despite the land ownership of colonies and the area as a whole, it is possible that sizable mortality can directly (roadkills, shooting) or indirectly be related to human presence. Surveys of public and landowner attitudes need to be conducted.

Conclusions

If BFFs are translocated to Montana, the CMR+SC (I+II) complex is the best candidate. It has the highest ranked habitat suitability (Table 3), its potential for prairie dog expansion is good, and land ownership is likely to be stable with low resource conflict in the future. Its location relative to nearby complexes and colonies offers prospects of future BFF expansion and interchange with the possible result of BFF establishment throughout the cluster of complexes in Phillips Resource Area. An additional benefit of neighboring complexes is the reduced risk of regional extirpation from stochastic events such as disease.

Figure 11.—Breakdown of colony acreage by land ownership within each proposed complex in Phillips Resource Area for 1988.



AUTHORS NOTE

After this document was completed, Biggins et al. (1988) was revised (Biggins et al. 1989). The variable D (Burrow Density) has been replaced by prairie dog density and the Rating Index (R) of a complex can now be thought of as an estimate of the total number of breeding female ferrets (with litters) it can support. Prairie dog density estimation for candidate complexes is based on several regression relationships involving active prairie dog burrow densities with predicted prairie dog density estimates from sample data. Their are no variables addressing spatial attributes. Assuming that the new Rating Index of Biggins et al. (1989) will be reviewed and accepted, we suggest that it replace V5, which summarizes food and reproduction, and remain a separate variable from our revised HSI. The revised HSI would therefore not include a food and reproduction variable but V3 (Burrow Density) would remain as a variable summarizing the cover value of burrows. As a consequence, V3 should have less weight in the revised HSI, say one half. With these alterations we think the Rating Index (summarizing food and reproduction) should be used in tandem with the HSI (summarizing spatial attributes, complex size (V2), and cover) for a more comprehensive evaluation of complexes.

In June, 1989, this data set was updated and Tables 2 and 3 were revised to reflect substantial colony increases. These increases were mostly due to additional inventory efforts rather than colony expansion. To receive these tables, write Steven Minta, Box 277, Whitefish, MT 59937.

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Plague in Prairie Dog Ecosystems: Importance for Black-footed Ferret Management

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Abstract.—Prairie dog numbers and the area covered by their colonies in the western United States declined drastically between 1900 and 1970 as a result of government pest control and probably plague epizootics. Concomitant with the reduction in area of prairie dog colonies, the black-footed ferret (*Mustela nigripes*), which depends on prairie dogs for prey, also disappeared from most of its former range. Black-footed ferrets are now being bred in captivity in hopes that they can be restored to areas of their former range where they are now extirpated. Because of the ferret's dependence on prairie dogs for food and their burrows for shelter, plague epizootics in prairie dog colonies are a serious problem for ferret management. In this paper the plague literature, as it pertains to prairie dogs, is reviewed. Known differences between the response of different prairie dog species' to plague are described, and several areas where future research might provide insights useful for prairie dog management are explored. The most important basic research questions for management of the prairie dog plague ecosystem are: (1) how is plague maintained in the prairie dog ecosystem between epizootics, and (2) how are plague epizootics in prairie dog colonies started? Answers to these related questions should help to decide where ferret reintroductions are most likely to be successful, and make it possible to predict when plague epizootics in particular prairie dog colonies are likely to begin.

In the late 1800s, Merriam estimated that 700,000,000 ac (283,000,000 ha) were occupied by prairie dogs in the western United States. By 1971, that area declined to 1,500,000 ac (600,000 ha, Cain et al. 1971, *in* Fagerstone and Biggins 1986). Although prairie dog eradication efforts by government agencies greatly reduced prairie dog numbers, another factor that may have been of equal importance occurred simultaneously. This was the introduction of sylvatic (wild rodent) plague (*Yersinia pestis*) into the United States in 1899 (Barnes 1982, Gregg 1985). Plague often kills more than 99 percent of prairie dogs in affected colonies (see below). The combined effects of the government's eradication efforts and sylvatic plague have had a devastating effect on Gunnison's (*Cynomys gunnisoni*), black-tailed (*C. ludovicianus*), and white-tailed prairie dog (*C. leucurus*) populations. Plague epizootics are more thoroughly reported in Gunnison's prairie dogs than in other prairie dog species (Lechleitner et al. 1962, 1968, Fitzgerald 1970, Rayor 1985), but plague can also annihilate black-tailed (Barnes 1982, Ron Chesser, personal communication) and white-tailed prairie dog populations (Clark 1977, Williams, undated). In white-tails, the disease appears to spread more slowly than in the former two species (Clark 1977, Ubico et al. 1988, George Menkens, personal communication).

High rates of prairie dog mortality and the disappearance of plague from prairie dog colonies for years at a time implicate other mammal species in the epizootiology of plague. Any understanding of plague dynamics that will be useful for ferret management must include plague in the context of the entire mammal community, not just within the prairie dogs. "Although people disagree on how management should be carried out, most agree that management of the black-footed ferret is dependent upon management of the prairie dog" (Linder 1973:171). An integral part of prairie dog management in areas where plague is prevalent will be to understand community-wide plague dynamics to an extent that allows prediction of the onset of an epizootic, and makes it possible to retard the spread of plague between prairie dog colonies.

In the remainder of this paper I will attempt to: (1) discuss why plague is an important component of the ecological setting for black-footed ferrets that should be considered in managing the species; (2) review the literature on plague to the extent that it provides insights useful for prairie dog management; (3) describe plague epizootics in prairie dogs and consider the roles that other rodent species might play in the long-term maintenance of plague foci; and (4) point out several critical areas of plague ecology where additional research is most desperately needed. I hope this paper will provide some new management ideas, and also stimulate further research in plague ecology.

BLACK-FOOTED FERRETS

Black-footed ferrets (*Mustela nigripes*) were once found in prairie dog colonies from Canada to Mexico through the high plains and the Rocky Mountain regions of the western United States. However, during the first half of the twentieth century the species disappeared from most of its former range (Hillman and Clark 1980). When black-footed ferrets were discovered near Meeteetse, Wyoming in 1981, plans were made to establish a captive breeding program that would make it possible to establish new populations in historic portions of their range where they are now extirpated (Carr 1986). Black-footed ferrets are nearly obligate predators on prairie dogs, subsisting on them, and using their burrows for shelter (Sheets et al. 1971, Gates 1973, Hillman and Linder 1973, Hillman and Clark 1980, Stromberg et al. 1983, Clark 1986). Black-footed ferrets may occasionally take other prey, but except for transients, ferrets have always been found in association with prairie dogs.

At Meeteetse the white-tailed prairie dog colonies that supported ferrets underwent a plague epizootic that began during the winter of 1984-1985. At that time black-footed ferrets began to disappear, presumably as a result of either starvation or canine distemper, which subsequently reached epizootic proportions in the black-footed ferret population (Forrest et al. 1988, Williams et al. 1988). Plague is not thought to be directly responsible for the loss of ferrets at that time, because many carnivore species, including domestic ferrets (*M. putorius*) and Siberian polecats (*M. eversmani*), appear to be resistant to plague (Willi-

ams, undated). To my knowledge black-footed ferret sera have not been tested for plague antibodies because of the risks involved in handling such a rare species.

Ultimately, it makes no difference if plague kills black-footed ferrets directly or by destroying their prey base. If black-footed ferrets are to be successfully restored to their historic range they must have a prey base that is consistent enough to secure long-term survival. Stable prairie dog populations may exist in areas outside of the range of plague, or where the transmission of plague is slow enough to allow populations to maintain themselves through an epizootic. Such maintenance might be possible where critical flea vector species are rare or missing, where prairie dogs occur at low enough density that contact with infected conspecifics is unlikely, or if the species develops some resistance to plague.

WILD RODENT PLAGUE IN THE UNITED STATES

Plague is a disease that is transmitted by flea vectors and found primarily in wild rodents. The etiologic agent is *Yersinia pestis*, "a Gramm-negative bipolar staining coccobacillus of the family Enterobacteriaceae" (Poland and Barnes 1979). Plague was probably introduced to the U.S. from Asia circa 1899 (Barnes 1982, Gregg 1985). The first record of plague in native mammals in North America was near Berkeley, California in 1908 among California ground squirrels (*Spermophilus beecheyi*, Wherry 1908). Since then the disease has spread throughout the western states west of the 100th meridian (Poland and Barnes 1979). Plague has been identified in eight orders of mammals worldwide (Poland and Barnes 1979), and in the U.S. plague has been identified in 76 species belonging to five mammalian orders: Rodentia, Lagomorpha, Insectivora, Artiodactyla, and Primates (Barnes 1982).

Plague ecology is poorly understood in part because of the complexity that results from the number of species involved. The potential for extensive human involvement has resulted in considerable research on plague ecology during the past 80 years. The disease occurs in foci or nidi (Pavlovski 1966) at various locations around the world, including North America, where the disease is recurrent and appears to be persistent. There are also non-focal areas where plague appears to be periodically reintroduced from outside and then disappears between epizootics (Poland and Barnes 1979).

Plague epizootics may be dramatic and frequently involve diurnal rodents, mostly ground squirrels or prairie dogs of the family Sciuridae. Many Sciurids, including prairie dogs, reach high population densities and are easily visible. Thus, when epizootics occur they are noted and investigated. Epizootics among these species may spread over hundreds of square miles (Barnes 1982). It is during or shortly after such epizootics that human plague cases most frequently occur (Weber 1978). Consequently the epizootic phase of the plague cycle has received a great deal of attention from public health organizations and is the source of most of the current knowledge of plague ecology.

The conventional wisdom among plague ecologists is that enzootic or maintenance species are likely to be "... moderately to highly resistant rodent species with little or no overt disease (Baltazard 1953, Baltazard et al. 1963, Kartman, Prince, Quan and Stark 1958) . . ." (Barnes 1982:238). California voles (*Microtus californicus*) in San Mateo County, California, south of San Francisco, fit these criteria in that they are capable of sustaining plague infections without overt symptoms, although there is some variance among individuals in response. California voles were found able to survive without symptoms with plague bacteremia capable of infecting fleas (Hudson et al. 1964, Goldenberg et al. 1964) This California vole system is the only verified example of an enzootic species despite many years of research on the topic. Other North American species that are thought to serve as enzootic hosts are kangaroo rats (*Dipodomys* spp.), deermice (*Peromyscus maniculatus*, Holdenried and Quan 1956), and northern grasshopper mice (*Onychomys leucogaster*, Thomas et al. 1988), which are moderately to highly resistant to plague and therefore potential enzootic hosts. All of these species are found within prairie dog colonies and may serve as a reservoir for plague between the epizootics seen in prairie dogs.

Furthermore, it appears that some species are evolving a reduced susceptibility to plague. Individuals from populations of several species with a history of plague have higher survival when exposed to plague in the laboratory than do individuals from plague-naive populations (Shepherd et al. 1986, Williams et al. 1979, Thomas et al. 1988). For example, California ground squirrels have begun to show higher rates of survival during epizootics in some areas of California than they did early in the century (Meyer et al. 1943, Nelson 1980). Rock squirrels (*Spermophilus variegatus*) have also developed resistance where contact with plague has been continuous compared to areas in Utah where plague has not been identified in this species (Marchette et al. 1962 [in Quan et al. 1985]). Variance in susceptibility to plague in rock squirrels (Quan et al. 1985), California squirrels (Williams et al. 1979) and northern grasshopper mice (Thomas et al. 1988) is also great.

As resistance develops, species' roles may shift from epizootic to enzootic status. If that happens, areas that infrequently experience plague today could become enzootic foci in the future, with obvious implications for prairie dog management. Thus the ecology of plague in North America may be changing rapidly today because of evolutionary changes in resistance within the host mammal community.

Another consideration concerns the relative importance of mammals versus fleas in the long-term maintenance of plague. In some other zoonotic diseases, such as LaCrosse encephalitis, the virus is maintained by the insect vector, and the mammalian hosts are thought to serve primarily to infect new insects (DeFoliart 1983).

The shift from epizootic to enzootic will not occur because of increased adult survival *per se*, because animals that survive should be immune. From the perspective of the bacteria, immunity is similar to host death. The important factor is that the immune individuals can reproduce and bring new susceptible individuals into the population. The ability of a population to maintain a disease is a function of the rate of disease transmission and the proportion of the population that is susceptible. The susceptible fraction of the population is a function of the reproductive rate of susceptible and immune adults.

PLAGUE IN PRAIRIE DOGS

Plague was first observed in Gunnison's prairie dogs in northwestern Arizona in 1932 (Eskey and Haas 1940). It appeared in Gunnison's prairie dogs in eastern Arizona in 1937 and in New Mexico in 1938 (Eskey and Haas 1940). It was first recorded in Utah prairie dogs (*C. parvidens*) in Utah, and white-tailed prairie dogs in Wyoming in 1936 (Eskey and Haas 1940). The first report of plague in black-

tailed prairie dogs was from near Lubbock, Texas, in 1946-47 (Miles et al. 1952). In Colorado, the first report of plague in prairie dogs was between 1945-49 when an epizootic occurred in Gunnison's prairie dogs at South Park (Ecke and Johnson 1952). Plague has now spread throughout the range of Gunnison's prairie dogs in Arizona, Utah, New Mexico and Colorado (Barnes 1982). It also persists in white-tailed prairie dogs in Wyoming (Clark 1977, Clark et al. 1985, Ubico et al. 1988) as well as in Utah and black-tailed prairie dogs (Barnes 1982). The progress of plague epizootics in black-tailed (Barnes 1982) and Gunnison's prairie dogs can be very fast and cover vast areas (Ecke and Johnson 1952, Lechleitner et al. 1962, 1968, Fitzgerald 1970, Barnes 1982, Rayor 1985, Cully et al. *in ms.*).

The rate of spread of epizootics appears to be in part a function of host population density (Barnes 1982, Cully et al. *in* ms.), although other factors such as flea species, flea density and host susceptibility may also be important. There are no data on the effects of the latter factors on the rate of epizootics in prairie dogs. White-tailed prairie dogs occur in much lower density colonies than black-tailed or Gunnison's prairie dogs (Eskey and Haas 1940, Clark et al. 1985, Menkens and Anderson, in press). Colonies may be isolated from other colonies or they may occur in complexes as at Meeteetse, Wyoming (Clark et al. 1986), or the Shirley Basin white-tailed complex south of Casper, Wyoming (Orahona and Anderson 1986).

A plague epizootic in white-tailed prairie dogs in 1967 in southeastern Wyoming killed 85 percent of the prairie dogs in 4 months (Clark 1977). At Meeteetse, Wyoming, a plague epizootic swept through four of 37 prairie dog colonies (Menkens and Anderson 1986), but these four colonies included 3756 ac (1521 ha) of the 7398 ac (2995 ha) of active prairie dog colonies in the complex (Clark et al. 1986).

Plague positive fleas have continued to be collected from prairie dog burrows at these colonies since 1985 (George Menkens, personal communication), but the epizootic does not appear to be spreading to other colonies. The total mean prairie dog density at four white-tailed prairie dog colonies at Meeteetse was estimated to be 1.5/ac (3.8/ha, Clark et al. 1985), which compares well with 1.4/ac (3.4/ha) in southern Wyoming (Clark 1977), and 1.4/ac (3.56/ha) in Colorado (Tileston and Lechleitner 1966).

Menkens and Anderson (in press) studied populations of white-tailed prairie dogs at six colonies that were selected for their high density (three colonies at Meeteetse) or lack of human disturbance (three near Laramie, Wyoming). During three years at Meeteetse they recorded a mean *adult* density of 1.7/ac (4.1/ha). At Laramie, over four years they recorded a mean *adult* density of 2.1/ac (5.1/ha). The high white-tailed prairie dog densities recorded by Menkens and Anderson (in press) are approximately 1/4-1/3 as high as adult densities of Gunnison's prairie dogs at the Moreno Valley, New Mexico prior to plague epizootics.

Black-tailed prairie dogs' ecology and social behavior has been more intensively studied than the other prairie dog species, yet reports of plague in this species are not nearly as well documented as in Gunnison's prairie dogs. The most detailed and long-term studies of black-tailed prairie dog behavior and ecology have occurred at Wind Cave National Park in South Dakota where plague has never been reported in prairie dogs (King 1955, Koford 1958, Hoogland 1979, 1981a, b, Hoogland and Folze 1982, Garret et al. 1984, Garrett and Franklin 1988). Miles et al. (1952) describe epizootics of plague in black-tailed prairie dogs near Lubbock, Texas between 1945-49, and plague epizootics still occur there today (Ron Chesser, personal communication). Extensive plague epizootics have occurred in black-tailed prairie dogs in eastern Colorado (Barnes 1982), but apparently plague has not occurred in this species north of Colorado. The reasons why plague has not struck northern black-tailed prairie dogs is unknown. Plague has been identified in other species in eastern Montana and Wyoming in counties where black-tailed prairie dogs occur (Barnes 1982), but not in the prairie dogs themselves. It is possible that epizootics in black-tailed prairie dogs have occurred but have not been noticed because of the remote locations of colonies.

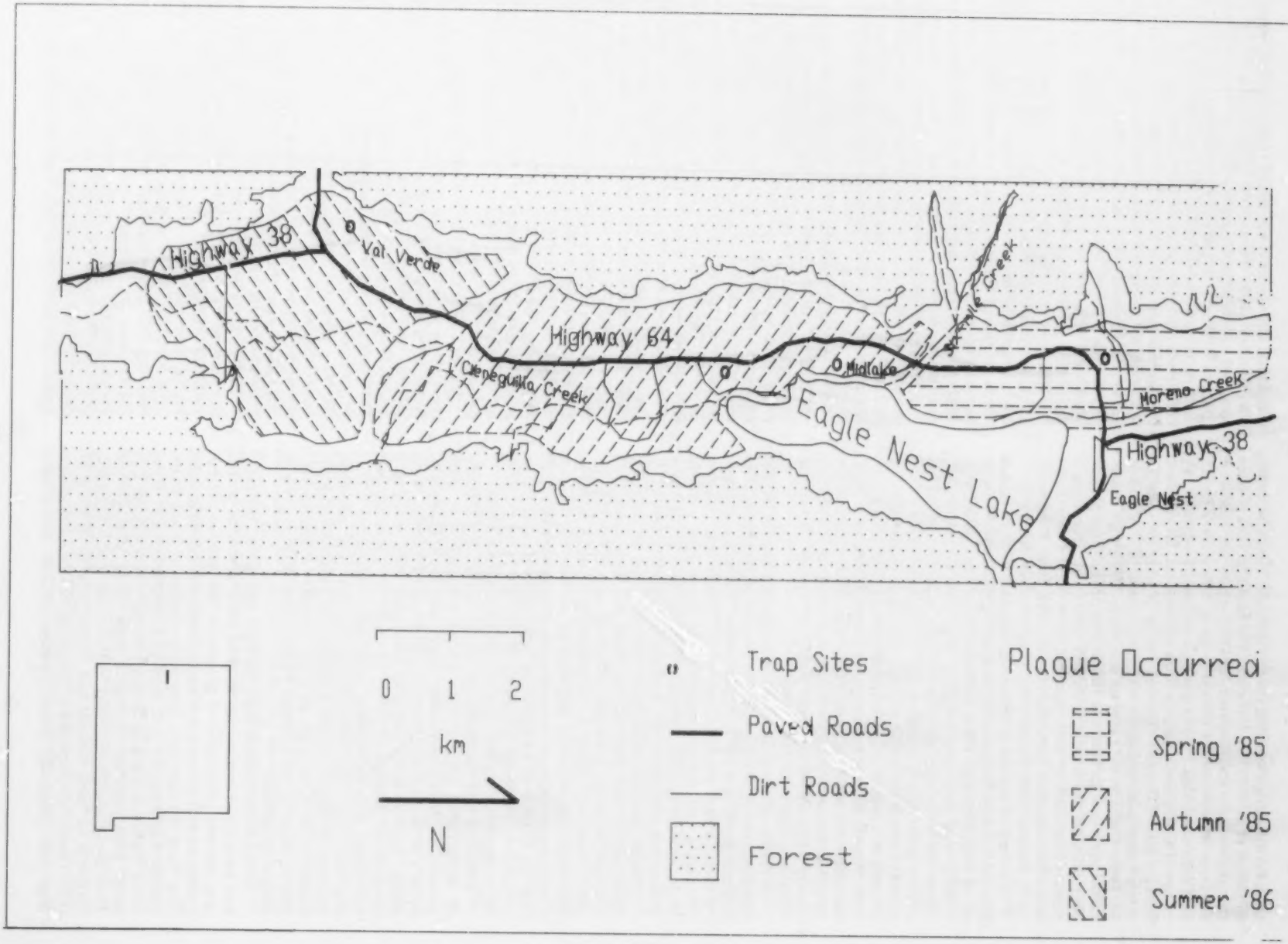
Gunnison's prairie dogs occur at densities that are often as high as black-tailed prairie dogs, and Gunnison's prairie dog populations are often very large (Ecke and Johnson 1952). In South Park, Colorado, Gunnison's prairie dog colonies covered more than 915,000 acres (370,000 ha) in 1941. At that time the Fish and Wildlife Service began prairie dog control activities and workers reported that "some disease" killed prairie dogs on more than 240,000 ac (97,000 ha) prior to poisoning. Between 1947 and 1949 in South Park, plague reduced prairie dog colonies to less than 5 percent of their former extent (Ecke and Johnson 1952).

The epizootic at South Park was the most spectacular reported for prairie dogs, but it is not necessary for Gunnison's prairie dog colonies to be large in order to become the focus of an epizootic. Lechleitner et al. (1962) watched a colony of approximately 275 Gunnison's prairie dogs go extinct in an isolated mountain meadow near South Park between June and September 1959. Likewise, Lechleitner et al. (1968) observed the passage of a plague epizootic through a complex of seven Gunnison's prairie dog colonies in Saguache Co., Colorado, between 1964-1966. Two of the colonies were eliminated during the first summer, and three more went extinct by 1966. There were a few prairie dogs remaining at two colonies when the epizootic ended in 1966. Fitzgerald (1970) began a study of Gunnison's prairie dogs in 1965 at South Park, Colorado. His colony was isolated by 8 mi (12.8 km) from other Gunnison's prairie dogs. The colony covered 11.7 ac (4.74 ha) and consisted of 68 prairie dogs in the summer of 1965. In two years, a combination of plague mortality and winter loss resulted in the extinction of the town.

Rayor (1985) observed a plague epizootic in a marked population of Gunnison's prairie dogs at the Curecanti National Recreation Area near Gunnison, Colorado. She reported the total annihilation of a colony of 1,000-1,500 prairie dogs during a 2 month epizootic in the spring of 1981. Some animals were still present in shrubby habitat surrounding her Blue Mesa study area after the epizootic (Barnes, personal communication), so apparently there were either some survivors or else prairie dogs recolonized the area very soon after the resident population was destroyed. I visited the Blue Mesa site in July 1986 and prairie dogs were again abundant despite control efforts.

An epizootic in Gunnison's prairie dogs swept through the Moreno Valley in north-central New Mexico between 1983-1987 (Cully et al. *in* ms.). The epizootic probably began near the town of Eagle Nest (Figure 1) where a human case occurred in August 1983. Surveillance by the New Mexico Environmental Improvement Division and the Centers for Disease Control, Plague Branch, found plague-positive fleas of species that associate with Gunnison's prairie dogs, thirteen-lined ground squirrels, and deermice. In October 1984 there were few prairie dogs near Eagle Nest, however, prairie dogs were abundant through-

Figure 1.—Map of the Moreno Valley in north-central New Mexico.



out the west and south of the Valley. At a study area between Eagle Nest Lake and U.S. Highway 64 (Midlake) where prairie dogs were marked and trapped in October 1984, the density was 12.1/ac (30/ha). Using the marked population as a guide to density at other areas, and a survey of colonies in the valley, Cully et al. (*in* ms.) estimated that the Gunnison's prairie dog population in the Moreno Valley at that time was more than 100,000.

North of Six-mile Creek and west of Moreno Creek in October 1984, prairie dogs were as abundant on the sides and tops of ridges as they were at Midlake. In March and April 1985, 5-6/ac (12-15/ha) emerged from hibernation at Midlake. Some of the missing prairie dogs may have emigrated, but many probably died of natural causes during hibernation (Cully 1985). Visual comparison of populations north of Six-mile Creek with the population at Midlake indicated that the population in the north was only 1.2-1.6/ac (3-4/ha) in March and April, and by 1 July 1985 the density was less than 1 per 25 ac (10 ha). Subsequent serology tests of survivors indicated that plague had been present (Cully et al., *in* ms.).

There were no indications of plague in prairie dogs at Midlake until July 1985; however, a large, but uncounted, population of thirteen-lined ground squirrels that had been present in October 1984 was reduced to two animals in April 1985. In July 1985, a blood sample was taken from an adult female prairie dog that had a weak serum antibody titer. On 21 July 1985, an adult male became sick and died in a trap, presumably of plague although that was not confirmed, and in August plague-positive fleas were collected from prairie dogs and their burrows. By 1 October 1985, the marked prairie dog population, which consisted of 168 animals in July, was reduced to approximately 25. Although it is possible that some of the animals missing in October were hibernating, only seven prairie dogs emerged from hibernation in March 1986, and all had disappeared by 1 July that year. On 1 September 1986, a careful search of 500 ac (200 ha) between Eagle Nest Lake and Highway 64 found two prairie dogs (Cully et al. *in* ms.).

The pattern at the north and center of the valley was repeated in the south with minor differences during 1986-1987. After the epizootic had spread through the Moreno Valley in June 1987, the entire Gunnison's prairie dog population in the valley was estimated to be 250-500 prairie dogs (Cully et al., *in* ms.). This figure includes several colonies in the north that had undergone 2 years of population growth at that time. Using the conservative estimate of 100,000 prairie dogs in October 1984, and 250-500 in June 1987, plague reduced the Gunnison's prairie dog population by 99.5 to 99.8 percent.

All of the above studies of plague in Gunnison's prairie dogs involved isolated colonies or colonies that were in isolated complexes. Climatic conditions and prairie dog flea species (*Opisocrostis hirsutus, O. labis, O. tuberculatus cynomuris*) involved in every case were similar, and in all cases prairie dog population declines were reported between 95-100 percent. In the Moreno Valley, fleas that associate with other rodent species were common in prairie dog burrows. At the end of epizootics many prairie dog fleas were infectious for plague. In addition, two *Thrassis bacchi*, thirteen-lined ground squirrel fleas, one *Rhadinopsylla sectilis*, and one *Monopsylla wagneri*, deermouse fleas (Haas et al. 1973), that were positive for plague were also taken from prairie dog burrows (Cully et al. *in* ms.).

Fitzgerald treated one-half of the colony that he studied with malathion to try to kill the fleas and stop the epizootic. His efforts may have slowed the spread of plague, but they were not successful in stopping the epizootic. At Meeteetse, progress of the plague epizootic may also have been slowed by insecticide treatment of some burrows to kill fleas. In 1985, selected burrows were treated with carbaryl dust (Menkens and Anderson 1986, Ubico et al. 1988), and it is possible that that effort reduced flea density below the numerical threshold necessary for the rapid spread of plague; however, this is not supported by field observations (George Menkens, personal communication). Laboratory study has demonstrated that white-tailed prairie dogs are highly susceptible to plague, so it is not likely that the epizootic stopped because the prairie dogs were resistant (Williams, E.S. undated report).

It is clear that Gunnison's prairie dogs are not the maintenance species for plague. At most, the species serves to rapidly spread the disease over large areas and possibly allow plague to infect new, potentially enzootic populations of other species. Maintenance of the disease has to be by other species (Lechleitner et al. 1962, 1968, Fitzgerald 1970, Barnes 1982, Cully et al. *in* ms.). It is interesting that white-tailed prairie dogs are able to maintain populations through plague epizootics while the more social black-tailed and Gunnison's prairie dogs cannot (Miles et al. 1952, Lechleitner et al. 1962, 1968, Fitzgerald 1970, Barnes 1982, Rayor 1985, Cully et al. *in* ms.). This appears to be a real difference between white-tailed and Gunnison's prairie dogs in that all of the above cited studies of Gunnison's prairie dogs started with apparently healthy populations that were selected to conduct long-term behavioral ecology studies.

GAPS IN KNOWLEDGE AND RESEARCH NEEDS

Some of the management problems created by plague in prairie dogs are: (1) how to predict whether a complex of prairie dog colonies will persist through time with a stable enough population to support a population of black-footed ferrets. (2) It would be convenient to be able to know in advance when an epizootic is going to occur so that ferrets could be moved, or other mitigation could be started. (3) If we understand how plague is spread within and between colonies, it might be possible to slow the rate of epizootics, and to reduce the probability of spread to adjacent colonies within a complex.

The first and most serious gap in knowledge of plague ecology is what happens to the disease between epizootics. Plague has been recorded in non-epizootic rodents, but except for the California vole system described above, plague is present in populations for a time and then apparently disappears (Poland and Barnes 1979, Barnes 1982). The Center for Disease Control, Plague Branch, in Ft. Collins, Colorado, monitored plague antibodies in badgers (*Taxidea taxus*), but after 8 years of positive records, the disease disappeared (Barnes, personal communication). During that time deermice were thought to be the maintenance hosts. Lechleitner et al. (1968) and Fitzgerald (1970) implicated deermice as an enzootic species. Richardson's ground squirrels (*S. richardsoni*, Lechleitner et al. 1962), woodrats (*Neotoma* sp., Miles et al. 1952, Barnes 1982), and meadow voles (Cully et al. *in* ms.) have also been implicated, but no direct evidence that any of these species maintain the disease has been reported.

Most plague epidemiology models assume that enzootic populations are spatially homogeneous. That is, that there is no spatial structure in the habitat that can cause variance in rates of contact between individuals in subpopulations or patches. This assumption is clearly unrealistic in

natural rodent communities where contact between individuals within patches is more likely than contact between individuals from different patches. Cully (1986) developed a hypothetical model for the enzootic maintenance of plague in the Moreno Valley, New Mexico, that does not depend on resistent maintenance populations. That model proposes that deermice and/or meadow voles are enzootic at that focus. Because of the spatial distribution of habitat patches used by these species, the complex social and population dynamics within patches, and dispersal between patches, if there are time lags between colonization of patches by healthy individuals and the appearance of plague at those patches via immigration of infected individuals, plague might be maintained by highly susceptible species. Deermouse population biology is ideally suited to the dynamics of this plague model (Cully 1984). If the model is correct, it could be very difficult to detect enzootic plague, even at known foci, because it would only be present in a given patch at unpredictable times. Because deermice and voles are not conspicuous, epizootics in these species could go unnoticed.

At Meeteetse, where the plague epizootic in white-tailed prairie dogs waned while many prairie dogs were alive, prairie dog density was low, burrows were widely dispersed, compared to Gunnison's and black-tailed prairie dogs, and more than 100,000 burrows were dusted in an attempt to stop the epizootic. Although plague-positive fleas continued to be found in burrows, it is possible that the dusting reduced the flea population below the vector transmission threshold (MacDonald 1957). It is also possible that with slow transmission among prairie dogs due to low prairie dog density and less frequent contact between prairie dogs, flea survival between mammal infections is maintaining plague in an enzootic state with white-tailed prairie dogs as the maintenance mammalian host. Continued plague research at Meeteetse should consider this possibility.

There are a number of other ways that plague could be maintained between epizootics. Plague could be maintained as free bacteria in the soil, by fleas or their eggs in unoccupied burrows (Kartman et al. 1958, Poland and Barnes 1979), or the disease could change to an avirulent form and be maintained by epizootic or other species (McEvedy 1988).

If the characteristics of the plague bacteria changed between a virulent epizootic form, and an avirulent enzootic form, the inoculation tests used to detect plague in fleas would not work, but the infected animals should still seroconvert, with the result that plague antibodies could be identified in blood samples. Surveys of prairie dog and other rodent species should be modified to search for avirulent forms of plague, particularly between epizootics (Poland and Barnes 1979). If this type of change in virulence occurs, laboratory studies could be initiated to identify the mechanism of change.

Plague bacteria may be able to survive for long periods in soil (Karimi 1963, in Poland and Barnes 1979) and directly infect prairie dogs, but there are several reasons why this is an unlikely mechanism for maintenance between epizootics. First, epizootics in prairie dogs and ground squirrels occur at 3-5 year intervals (Barnes 1982, Cully et al. *in* ms.) which is too long a time for the bacteria to survive outside of hosts. Second, if the bacteria were present in the soil, prairie dogs should succumb soon after recolonizing an infected town. This does not seem to happen in that Gunnison's prairie dogs have been found in burrows less than 1 year after epizootics. Many of those animals were sero-positive for plague however, so they may have been immune. Their offspring the following year did not become infected either, however, and they were not immune. Third, if soil bacteria were the source of bacteria to begin epizootics, most epizootics should begin when the animals have the most skin injuries; that is during the breeding season. Although some epizootics have been reported at that time (Rayor 1985, Cully et al. *in* ms.), most have begun in summer after the young emerged from their natal burrows.

Plague-infected fleas are the primary vectors of plague, and are probably responsible for infecting most prairie dogs after an epizootic begins. Infected fleas have a long survival time in the lab where plague-infected fleas have survived for more than a year at room temperature in dark conditions (Pavlovski 1966). Infected fleas have been removed from prairie dog burrows more than a year after the beginning of epizootics and at least several months after the disappearance of susceptible prairie dogs (Fitzgerald 1970, Cully et al. *in* ms.). Precise survival times under natural conditions in the field have not been determined because it is difficult to know when the last prairie dog in a colony dies or emigrates, and because as epizootics wane, the immune status of the survivors are unknown. Infected fleas without hosts cannot survive the 3-5 years between epizootics.

The most plausible mechanism for maintenance between sciurid epizootics is that other mammalian host species are involved. The California vole example cited above is a case in point. At San Bruno Mountain, San Mateo County, California, California voles may become infected like other rodents, and attain sufficient numbers of bacteria in their blood to infect fleas, yet show no overt symptoms of the disease (Hudson et al. 1964). Presumably after infection these animals are immune to further infection. By surviving they can continue to provide young naive voles via reproduction which provide a susceptible host population. In that system the rodents can produce several litters of offspring per year, so infected fleas can probably maintain plague during short periods when susceptible voles are not available. Such clear enzootic systems have not been identified elsewhere so the process of maintaining plague in other areas may be different.

The second major unsolved problem in plague ecology is how, when, and why plague is transmitted into prairie dog populations to start epizootics. If these problems can be resolved it should be possible to predict when an epizootic is likely to begin. Knowing the enzootic species is obviously critical to understanding how prairie dogs become infected. Transmission to prairie dogs at the beginning of epizootics could be initiated by contact with fleas that were infected by feeding on other bacteremic rodent species, by contact with prairie dog fleas transported from distant prairie dog colonies by raptors or wild carnivores (Fitzgerald 1970, Poland and Barnes 1979), or domestic dogs (Rust et al. 1971a,b), by eating plague-infected carrion (Rust et al. 1972), or by pneumonic transmission from other species (Rollag et al. 1981).

Assuming that plague is maintained by enzootic rodents and transmitted to prairie dogs by fleas, we need to know what variables increase the risks of transmission between species. There are few data on flea densities prior to epizootics in prairie dogs or other rodent species, but variance in flea density could alter the likelihood of interspecific transmission. There are also few data on the population dynamics of potential enzootic mammal species prior to epizootics, or on the changes in habitat overlap

that occur with changing rodent density. As the density of enzootic or epizootic species increases, habitat overlap with other species may increase, thus increasing the possibility of interspecific contact.

Plague ecology in most areas probably is affected by a complex interplay of the above factors. Focussing on only one aspect of the system probably will not provide insights useful to management. Flea density may be a function of host population density, and interspecific transmission of plague may be dependent on both habitat overlap of the rodent species, as well as on density of fleas on enzootic, epizootic, or both groups of rodents. Future research should consider these complexities.

Finally, I want to reiterate that because of the broad spectrum of habitats, and the extensive geographic area used by prairie dogs, details of plague ecology may differ among populations or species. Prairie dogs occupy a wide range of habitats with rodent species unique to each. Different rodent species have different habitat associations so the degree of overlap will vary. Each rodent species also carries different flea species, and different fleas may affect transmission by being more or less host specific, or effective as plague vectors. In some systems plague might be transmitted directly from enzootic to epizootic species, whereas in other systems intermediate hosts may be necessary. Thus, it may never be possible to draw broad generalities about plague ecology that can be transferred easily between prairie dog species, or even populations. Nevertheless, site specific information has the potential to determine whether black-footed ferret reintroductions will be successful.

SOME IMPLICATIONS FOR BLACK-FOOTED FERRET CONSERVATION

The first concern in choosing reintroduction sites for black-footed ferrets has to be that the complex of prairie dog towns selected will persist. Information available at this time is that plague can destroy colonies of black-tailed, white-tailed, Utah and Gunnison's prairie dogs, and make the colonies that are subject to plague unfit for black-footed ferret reintroduction. The exceptions seem to be that white-tailed prairie dogs at the Meeteetse complex in Wyoming, have persisted through a plague epizootic largely intact, and that black-tailed prairie dogs in the northern plains have not experienced plague. It is not known at this time why either of these phenomena should be true. If plague epizootics do occur in northern black-tailed prairie dog colonies, or if the severity of the epizootic at Meeteetse increases, current hopes for black-footed ferret recovery will suffer a major setback.

Lechleitner et al. (1968) suggest that Gunnison's prairie dogs' ability to maintain populations in nature is due to the rarity with which they are exposed to plague by enzootic species. Management of prairie dogs for black-footed ferrets will require prairie dog exposure to plague to be reduced, and that once an epizootic begins its spread can be slowed, at least between colonies. If prairie dogs develop greater variance in susceptibility to plague, as recorded in other species (Williams et al. 1979, Quan et al. 1985, Shepherd et al. 1986, Thompson et al. 1988), it may be possible to evolve resistance and maintain adequate populations of Gunnison's and black-tailed prairie dogs even while epizootics are in progress. If these management goals could be realized, it would be possible to expand the range of potential black-footed ferret recovery to include most of the species' former range. It is clear that continued research on plague ecology should be pursued aggressively as part of the black-footed ferret recovery program.

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